

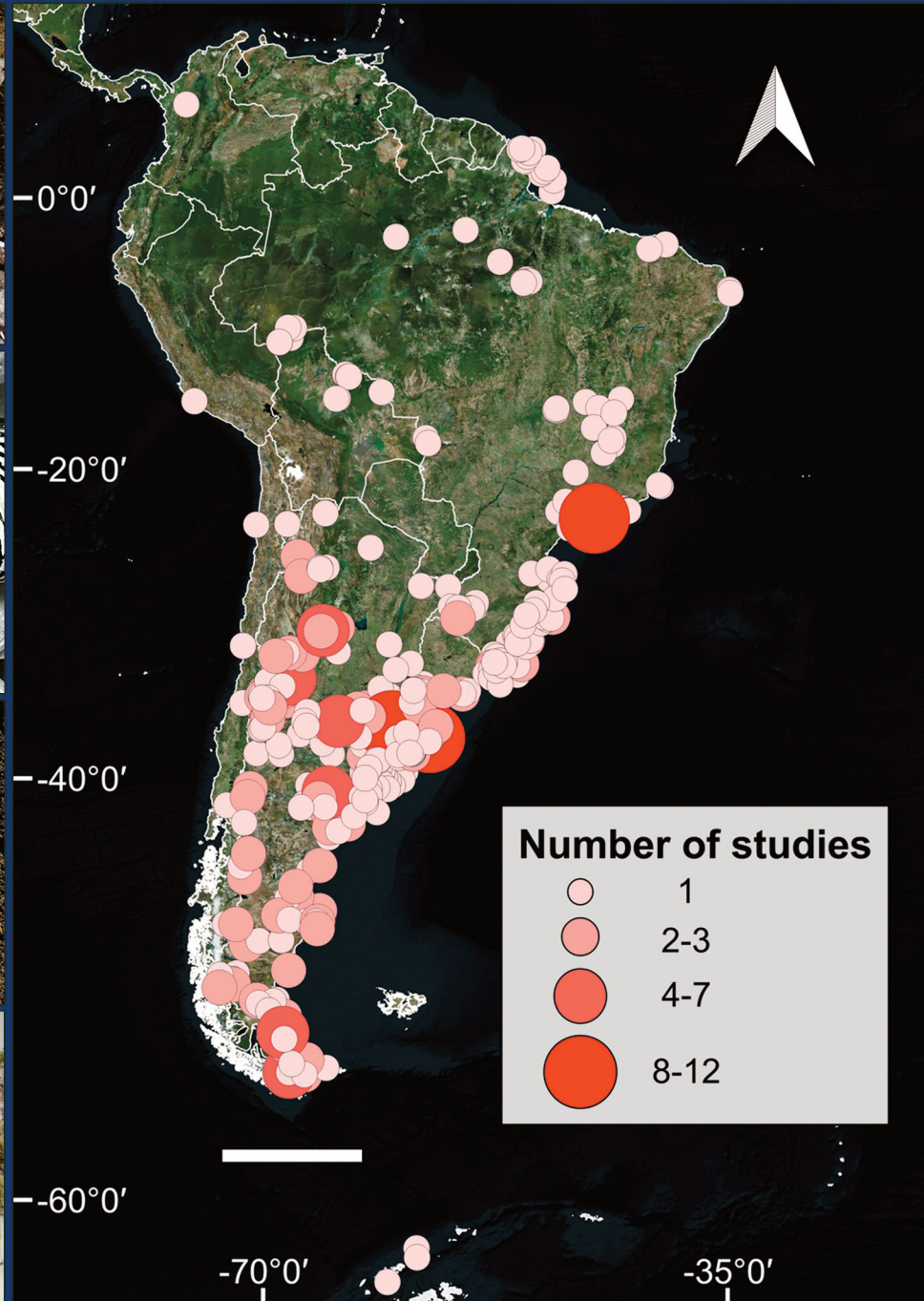


Publicación Electrónica

ASOCIACIÓN PALEONTOLÓGICA ARGENTINA

SOUTH AMERICAN PAPERS ON ACTUALISTIC TAPHONOMY

Editors: Gabriela Hassan and Karen Borrazzo



Asociación Paleontológica Argentina - Maipú 645 1° piso
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Te/Fax (54-11) 4326-7563



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www.apaleontologica.org.ar



ISSN 2469-0228

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Ciudad Autónoma de Buenos Aires

2025



ISSN 2469-0228

PROLOGUE

SOUTH AMERICAN PAPERS ON ACTUALISTIC TAPHONOMY

Taphonomy, since its formal definition by Efremov in 1940, has become a central pillar in paleontology, archaeology, and related disciplines. Although early paleontological works already incorporated insights on preservation, the coining of the term provided a framework for a systematic understanding of the processes affecting organic remains from the biosphere to the lithosphere. During the mid-twentieth century, taphonomic studies were often considered subsidiary to paleoecology, but the revitalization of the field came with the foundation of the journal *PALAIOS* in 1986 (Parsons-Hubbard *et al.*, 2011). This landmark not only promoted a new generation of studies focused on patterns and processes of fossilization but also consolidated the foundations of taphonomic research in both fossil deposits and modern settings. By emphasizing the actual processes that shape preservation, this shift laid the ground for what was later termed Actualistic Taphonomy (Martínez *et al.*, 2020). Since its early applications in Archaeology, the key role of actualism in taphonomic research (naturalistic observations and experiments; Marean, 1995) was noted (Gifford, 1981; Lyman, 1994). Indeed, the pioneer taphonomic zooarchaeological works in South America were actualistic studies (Nasti, 1984; Borrero 1985). Formerly restricted to the analysis of zooarchaeological assemblages, taphonomy nowadays provides a general framework for studying the formation processes that affect all the material remains (organic and inorganic) of the archaeological record (e.g., Dominguez-Rodrigo *et al.*, 2011; Behrensmeyer *et al.*, 2018; Borrero *et al.*, 2024).

The recognition that modern environments provide essential insights into preservation directly led to the rise of Actualistic Taphonomy (also referred to as neotaphonomy), which focuses on documenting and analyzing modern processes of decay, preservation, and burial as analogs to interpret the fossil and the archaeological records. Over the last decades, this approach has expanded considerably in South America, producing a wealth of case studies on plants,

invertebrates, vertebrates, trace fossils, and different types of archaeological remains. These investigations have broadened the methodological scope of the discipline and highlighted its interdisciplinary potential (Ritter *et al.*, 2016, 2023). Thus, Actualistic Taphonomy should not be understood merely as a methodological toolkit, but as a dynamic research field with broad implications across the life and earth sciences (Behrensmeyer *et al.*, 2018). Its consolidation in South America exemplifies the vitality of the field and the richness of regional research traditions that contribute to global debates.

The Workshop on Actualistic Taphonomy in South America (*Taller de Tafonomía Actualista en América del Sur, TAAS*) emerged as the interdisciplinary meeting organized by the South American School of Taphonomy (SST), a group of South American taphonomists interested in founding regional projects of collaborative research (Ritter *et al.*, 2016). The workshop brings together South American researchers, students and professionals from different disciplines devoted to understanding the natural and cultural processes of preservation and destruction involved in the fossilization processes or the formation of the archaeological record through the application of both naturalistic and experimental components of actualistic taphonomy research. The *TAAS* holds every three years, preferably varying the host country. The first *TAAS* was conducted in Montevideo, Uruguay in October 2017. This workshop included the participation of speakers from Argentina, Brazil and Uruguay, and the presentation of 20 works of biology, paleontology, geology, and archaeology. The contributions were published as a special volume in the *Topics in Geobiology* of Springer (Martínez *et al.*, 2020). The second *TAAS* was held virtually in July 2021, during the covid-19 pandemic. The organization was in charge of Brazilian colleagues and achieved 35 works from Argentina, Brazil and Uruguay. A selection of the papers presented was published in a special volume *PALAIOS* (38-3) in 2023. The Third

Workshop on Actualistic Taphonomy in South America (3TAAS) was conducted in Mar del Plata, Argentina, in October 2024, and in this edition a total of 32 works were presented. The first edition of the workshop in Argentina was characterized by an increase in multidisciplinary integration, with more archaeological participation, and a larger representation of terrestrial environments in the works presented (Hassan & Borrazzo, 2024).

The current volume of *Publicación Electrónica de la Asociación Paleontológica Argentina* brings together five contributions originally presented at the 3TAAS. Collectively, these works illustrate the vitality and diversity of current actualistic research in the region, spanning a wide range of organisms and archaeological materials, depositional environments, and interpretive scales. While each paper addresses specific case studies, together they highlight the integrative and interdisciplinary nature of taphonomic approaches, and their relevance for understanding both recent and ancient biotic and archaeological records, their taphonomic history and preservation.

The opening contribution by De Francesco and colleagues offers a conceptual and historic review on Actualistic Taphonomy in South America, underlining its foundations and its potential as a unifying framework across paleontological, archaeological, and ecological studies. Based on an extensive literature review, the authors demonstrated that initial studies in the region were mostly descriptive and opportunistic, often linked to paleontological surveys or archaeological contexts. However, a more systematic approach soon emerged, encompassing coastal and continental environments, marine and freshwater settings, and a wide range of organisms from plants and invertebrates to vertebrates as well as several archaeological materials. This regional growth has been characterized by the expansion of actualistic studies across a wide range of disciplines and materials, with archaeology and vertebrate research being the most prolific, followed by works on mollusks and lithics, while several other groups remain underexplored. Overall, this review highlights the advances achieved in South American Actualistic Taphonomy, while drawing attention to underrepresented environments and taxonomic groups that should be addressed in future studies.

The paper by Borrazzo and colleagues deals with the

genesis of an ephemeral biotic record of marine organisms dated to the Middle Holocene in northern Isla Grande of Tierra del Fuego (Argentina). The authors assess the natural or cultural origin of a thin shell lens (composed by bivalves, gastropods and fishbones) located ~3 km from the current coastline by examining the geomorphological evolution of the local landscape, the taxonomic composition and the taphonomic characteristic of the biotic assemblage, and the sedimentological and geochemical properties of the deposit. Based on naturalistic observations, geochronological background, pedolithological characteristics of the locus, ethnographic and regional archaeological information Borrazzo and colleagues conclude that the shell lens constitutes an anthropogenic deposit.

Martínez and colleagues provide a rare long-term actualistic perspective on freshwater shell assemblages by repeatedly sampling death assemblages of the invasive bivalve *Corbicula fluminea* in the Río de la Plata (Uruguay) across three campaigns spanning more than three decades. Their analysis shows that most taphonomic alterations occur rapidly after death, with little further modification over time. This finding challenges the notion of progressive, cumulative alteration and instead points to an early stabilization of preservational signatures. By using an invasive species with a well-documented introduction history as a natural experiment, this contribution demonstrates the potential of long-term monitoring to refine our understanding of shell preservation in fluvial environments. It also highlights the value of neotaphonomic studies in linking ecological dynamics, invasion biology, and the processes that govern the formation of the fossil records.

The neotaphonomic research led by Montalvo and colleagues provides analogues for interpretations on the origin of archeological and paleontological assemblages. The paper presents a detailed study of undigested and modified digested bone remains by the crowned eagle (*Buteogallus coronatus*). Bones and pellets were collected from nests of this raptor in the central-west La Pampa, Argentina. Among prey remains, the pellets include the osteoderms of two armadillos. Authors note that the osteoderms of *Zaedyus pichiy* recovered from the pellets exhibit modifications in their ornamentation and a reduction in thickness. Pellets also provide the first record of pink fairy armadillo (*Chlamyphorus*

truncatus) in the diet of crowned eagles. The extreme degree of modification shown by *C. truncatus* osteoderms highlights their low potential for preservation in the fossil record.

Borrero and colleagues undertake a long-term naturalistic taphonomic study of guanaco (*Lama guanicoe*) carcasses resulting from two winter die-offs in 2020 and 2023 in the Coyle-Gallegos River interfluvium (Santa Cruz Province, Argentina). By the longitudinal monitoring of carcass accumulations, the authors delve into the formation of averaged samples and the fossil record. They identified differential preservation conditions through the study area, with spaces offering from minimal to high burial possibilities. The authors note the occurrence of spatial overlapping of different mass death events and the formation of mixed assemblages of naturally deposited bones and archaeological materials. Their study provides fundamental data for constructing long-term viable analogous models of the archaeological and paleontological records.

Taken together, these contributions underscore the breadth of Actualistic Taphonomy in South America, from theoretical reflections to detailed case studies, and from short-term processes to multi-annual monitoring. They also demonstrate the importance of collaborative efforts such as the *TAAS* meetings, which foster the integration of diverse approaches and scales of analysis into a cohesive research program. The works gathered here not only reflect the maturity of actualistic studies in the region, but also reaffirm the value of collaborations that cross disciplinary and national boundaries. This continuity consolidates a regional network of taphonomic research and positions South

American Actualistic Taphonomy as a consistent contributor to global debates, with this volume standing as the most recent link in a sustained sequence of *TAAS* publications. Even though the Argentine edition of *TAAS* achieved higher levels of multidiscipline than previous editions, several fields currently conducting research in Actualistic Taphonomy remain underrepresented. Therefore, the future challenge for the *TAAS* is to increase the participation of South American scholars from disciplines that use present day observations and experiments to unravel the records of the past, such as forensic science and neoichnology. Recognizing the common grounds in Actualistic Taphonomy across the disciplines is key to building the theoretical and methodological bases for a transdisciplinary approach to study past life on Earth.

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SOUTH AMERICAN PAPERS ON ACTUALISTIC TAPHONOMY

Gabriela Hassan and Karen Borrazzo
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THE RISE OF ACTUALISTIC TAPHONOMY IN SOUTH AMERICA

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Abstract. Over the past four decades, global actualistic taphonomy studies have grown significantly, driven by increased interest in present-day patterns and processes of fossilization. South America has mirrored this trend, though the exact growth level is unclear. This study compiles actualistic taphonomy research in South America based on internationally accessible journal articles and book chapters using databases such as Web of Science, ResearchGate, Google Scholar, and Academia. Results revealed a steady rise in studies from 1985, with Argentina leading, followed by Brazil, Uruguay, and a few other countries with lesser representation. Terrestrial environments have seen the most extensive research, largely due to archaeologists and vertebrate paleontologists, with marine environments (mainly mollusk-based studies) following. Freshwater actualistic taphonomy began in 2006 and was the next most commonly represented, while estuarine and lagoonal environments were the least studied. Most research has been naturalistic: examining taphonomic patterns, taphofacies, live-dead fidelity, and time-averaging. However, experimental studies increased markedly after 2009. Synthesis papers appeared from 2007, reflecting the growing body of literature. Archaeological studies have been the most prolific, with vertebrate studies dominating the region's actualistic taphonomy literature, followed by research on mollusks and lithics. Brachiopods, foraminifera, diatom, pollen, and phytoliths have developed less. Several groups, including plants, arthropods, worms, lichens, charcoal, pottery, rock art paintings, and sediments, remained poorly studied, highlighting the need for further research. This review underscores the significant progress made in South American actualistic taphonomy but also points to underrepresented environments and taxonomic groups that should be addressed in future studies.

Key words. Naturalistic studies. Experimental studies. Multidisciplinary. Environmental diversity. Geographical distribution.

Resumen. EL CRECIMIENTO DE LA TAFONOMÍA ACTUALISTA EN SUDAMÉRICA. En las últimas cuatro décadas, los estudios de tafonomía actualista a nivel mundial aumentaron significativamente, impulsados por el creciente interés en los patrones y procesos modernos de fosilización. Sudamérica ha seguido esta tendencia, aunque el nivel exacto de crecimiento no está claro. Este estudio compila investigaciones de tafonomía actualista en Sudamérica, basadas en artículos de revistas y capítulos de libros accesibles internacionalmente, utilizando bases de datos como *Web of Science*, *ResearchGate*, *Google Scholar* y *Academia*. Los resultados revelaron un aumento constante en los estudios desde 1985, con Argentina a la cabeza, seguida por Brasil, Uruguay y algunos otros países con menor representación. Los ambientes terrestres recibieron la mayor cantidad de investigaciones, principalmente debido a arqueólogos y paleontólogos de vertebrados, seguidos por los ambientes marinos (mayormente moluscos). Los ambientes dulceacuícolas, que comenzaron a investigarse en 2006, fueron los siguientes más representados, mientras que los estuáricos fueron los menos estudiados. La mayoría fueron investigaciones naturalistas: patrones tafonómicos, tafofacies, fidelidad vivo-muerto y promediación temporal. Los estudios experimentales aumentaron notablemente desde 2009. Los artículos de síntesis surgieron en 2007, reflejando el creciente cuerpo de literatura. Los estudios arqueológicos fueron los más prolíficos, con los vertebrados dominando la literatura, seguidos por moluscos y líticos. Braquiópodos, foraminíferos, diatomeas, polen y fitolitos tuvieron menor desarrollo, y varios grupos, como plantas, artrópodos, gusanos, líquenes, carbones, cerámicas, pinturas rupestres y sedimentos, permanecen poco estudiados. Esta revisión subraya el progreso de la tafonomía actualista en Sudamérica y señala los ambientes y grupos taxonómicos subrepresentados que deberían abordarse en futuros estudios.

Palabras clave. Estudios naturalistas. Estudios experimentales. Multidisciplinario. Diversidad ambiental. Distribución geográfica.

ACTUALISTIC TAPHONOMY is a multidisciplinary field that studies present-day patterns and processes of decay and burial of organic material (for example, bones, shells, or soft tissues) for understanding the principles governing the fossilization, as well as the preservation of lithic tools, pottery, and other archaeological materials (Behrensmeyer *et al.*, 2018; Behrensmeyer, 2021; Borrero, 2020; Domínguez-Rodrigo *et al.*, 2011). By studying modern processes, the discipline gathers insights into interpreting historical data within the fossil record, allowing for more accurate reconstructions of past ecological and environmental conditions (Kowalewski & LaBarbera, 2004). Although the systematic development of actualistic taphonomy in South America began in the late 20th century, earlier examples of taphonomic thinking can be traced back to the 19th and early 20th centuries. Notably, Florentino Ameghino and Charles Darwin made observational remarks on fossilization processes that, although not framed within a formal taphonomic approach, anticipated later concepts (Pomi & Tonni, 2008; Borrero, 2009; Nahuel-Ruiz *et al.*, 2024). Over the past four decades, the field of actualistic taphonomy has achieved global acceptance, as evidenced by the substantial increase in scientific publications across a wide range of disciplines, including paleontology, archaeology, and forensic sciences (Behrensmeyer, 2021).

The research themes encompassed a wide range of subjects, including biostratigraphy, comparative taphonomy, taphofacies, live-dead fidelity, methodological biases, time-averaging, and conservation paleobiology, among others (Kowalewski & LaBarbera, 2004; Assumpção & Ritter, 2025). The approaches employed can be categorized as naturalistic or experimental in origin, as defined by Marean (1995). In the former, researchers used observations from natural patterns to establish relations between taphonomic agents and their effects on the material (Alunni & Álvarez, 2017). The experimental approaches performed have been field-based, entailing the exposure of remains to a natural environment and the assessment of preservation modes, or laboratory-based, involving procedures conducted within a controlled laboratory setting (Parsons-Hubbard *et al.*, 2011).

The preponderance of actualistic taphonomy studies has been centered in the Northern Hemisphere, with a

pronounced emphasis on mollusks and a predominant focus on marine and estuarine environments (*i.e.*, edited volumes by Kidwell & LaBarbera, 1993; Kowalewski & LaBarbera, 2004; Kowalewski & Rothfus, 2012). Conversely, South America is scarcely represented, despite its unparalleled environmental diversity and substantial paleontological and archaeological heritage (Ritter *et al.*, 2016). This discrepancy not only curtails our understanding of taphonomic processes in the Southern Hemisphere but also perpetuates a bias in formulating universal models, underscoring the pressing need to augment research endeavors in this region. Recent years have seen an uptick in actualistic taphonomy studies in South America, as evidenced by the publication of several synthesis works and thematic volumes (*e.g.*, Ritter *et al.*, 2016, 2023a; Alunni & Álvarez, 2017; Gutiérrez *et al.*, 2018; Mondini, 2018; Montalvo & Fernández, 2019; Martínez *et al.*, 2020). However, the question remains whether this signifies a transient phenomenon or a more extensive regional augmentation in research activity. To test this hypothesis, we reviewed actualistic taphonomy studies conducted in South America from their inception to the present.

MATERIALS AND METHODS

A comprehensive search of relevant international databases, including Web of Science, ResearchGate, Google Scholar, and Academia, was conducted to identify publications on actualistic taphonomy conducted in South America. These platforms were selected for their broad coverage of peer-reviewed articles, grey literature, and regionally relevant publications in paleontology, archaeology, and related disciplines. Although other databases contain valuable regional content, preliminary searches indicated that the most relevant studies indexed in these databases were also retrievable through our selected platforms. Nevertheless, we acknowledge that this selection may introduce a degree of publication bias. The compilation covered articles published in peer-reviewed scientific journals and book chapters with international reach. It is important to note that this study did not consider conference proceedings, abstracts, and theses.

The present study exclusively incorporates investigations that concentrate on actualistic taphonomy.

Taphonomic studies solely conducted on fossil (non-modern) successions were excluded, except when the study also included an actualistic sampling component. The main keywords used in the database searches contained 'taphonomy', 'actualism', 'taphonomic experiment', 'naturalistic', 'live-dead fidelity', 'time-averaging', 'taphofacies', and related terms in English, Spanish, and Portuguese. After retrieving the initial results, we thoroughly screened each article to confirm its relevance to original actualistic taphonomic research. We excluded studies that merely applied previously published actualistic data without contributing new observations, experiments, or syntheses, ensuring that our dataset reflected novel contributions to the field. However, this search strategy may limit the inclusion of studies that, although methodologically aligned with actualistic taphonomy, do not explicitly identify themselves using this terminology. As a result, certain areas—such as neoichnology or forensic sciences—may be underrepresented in our database despite addressing taphonomic processes through empirical and experimental approaches consistent with actualistic frameworks.

For each publication, the following data were collected: (a) publication year (up to 2023), (b) language (English, Spanish, or Portuguese), (c) journal (or publisher for books), (d) country of the study, (e) environment (marine, estuarine/lagoonal, freshwater, or terrestrial), (f) indicators analyzed (e.g., mollusks, vertebrates, pollen, lithics), (g) study type (naturalistic, experimental, synthesis, theoretical, or methodological), (h) study focus (paleontological, archaeological, or forensic), and (i) geographic location of the sampled sites (only studies classified as naturalistic or field-based experimental were considered here). In the case of laboratory-based studies conducted within the study region, the coordinates of the city where the research was performed were also included.

RESULTS

A total of 310 articles were identified (see Suppl. Inf. 1). Of them, 234 (75.5%) came from Argentina, 56 (18.1%) from Brazil, 9 (2.9%) from Uruguay, and 7 (2.3%) from Chile. The remaining articles (1.3%) corresponded to French Guiana, Peru, Bolivia, and Colombia. The results revealed an increase in actualistic taphonomy studies in South America from

1985 (the earliest record in our database) to the present. Argentina led this trend, followed by Brazil (which started in 1995) and Uruguay (Fig. 1). The remaining countries only had sporadic records. Most studies were conducted in the Southern Cone, particularly in Argentina, with the majority focused within the province of Buenos Aires (Fig. 2).

Terrestrial environments have seen the most extensive research (70.8%), mainly due to contributions from archaeologists and vertebrate paleontologists, with marine environments following (16.2%). Freshwater actualistic taphonomy, which began in 2006, was the next most represented (8.4%), while estuarine and lagoonal environments were the least studied (Fig. 3). Studies on terrestrial environments were mostly situated in the Southern Cone, especially in Argentina (Fig. 4). Both marine and estuarine/lagoonal environments were mainly located on the Atlantic coast, while freshwater environments had disjunct distributions, with studies conducted in Brazil, Bolivia, and the Pampas of Argentina (Fig. 4).

Most research (68.4%) has been naturalistic, mainly focusing on taphonomic patterns observed in the field, taphofacies, live-dead fidelity, and time averaging. Experimental studies (24.4%) began in 1991 and significantly increased after 2009. By 2007, synthesis works (4.7%) started to emerge, likely driven by the substantial accumulation of data. More recently, since 2016, general theoretical (1.2%) and methodological studies (1.2%) have also been published (Fig. 5).

Among naturalistic studies, those with archaeological objectives were the most developed in South America, playing a pioneering role in the discipline. In contrast, studies with a paleontological focus have experienced rapid growth since 2015 (Fig. 6). Geographically, naturalistic studies with archaeological objectives have been more prevalent in continental regions of Argentina. In contrast, those with paleontological objectives have been more commonly conducted in coastal areas (Fig. 7).

Vertebrates dominated the literature (54.9%), with mollusks ranking second (16.9%). Lithics were the third most represented indicator (8.1%). Foraminifera, brachiopods, pollen, diatoms, and phytoliths collectively accounted for a smaller proportion (14.1%). Many indicators, including plants, arthropods, lichens, worms, sediments, echinoderms,

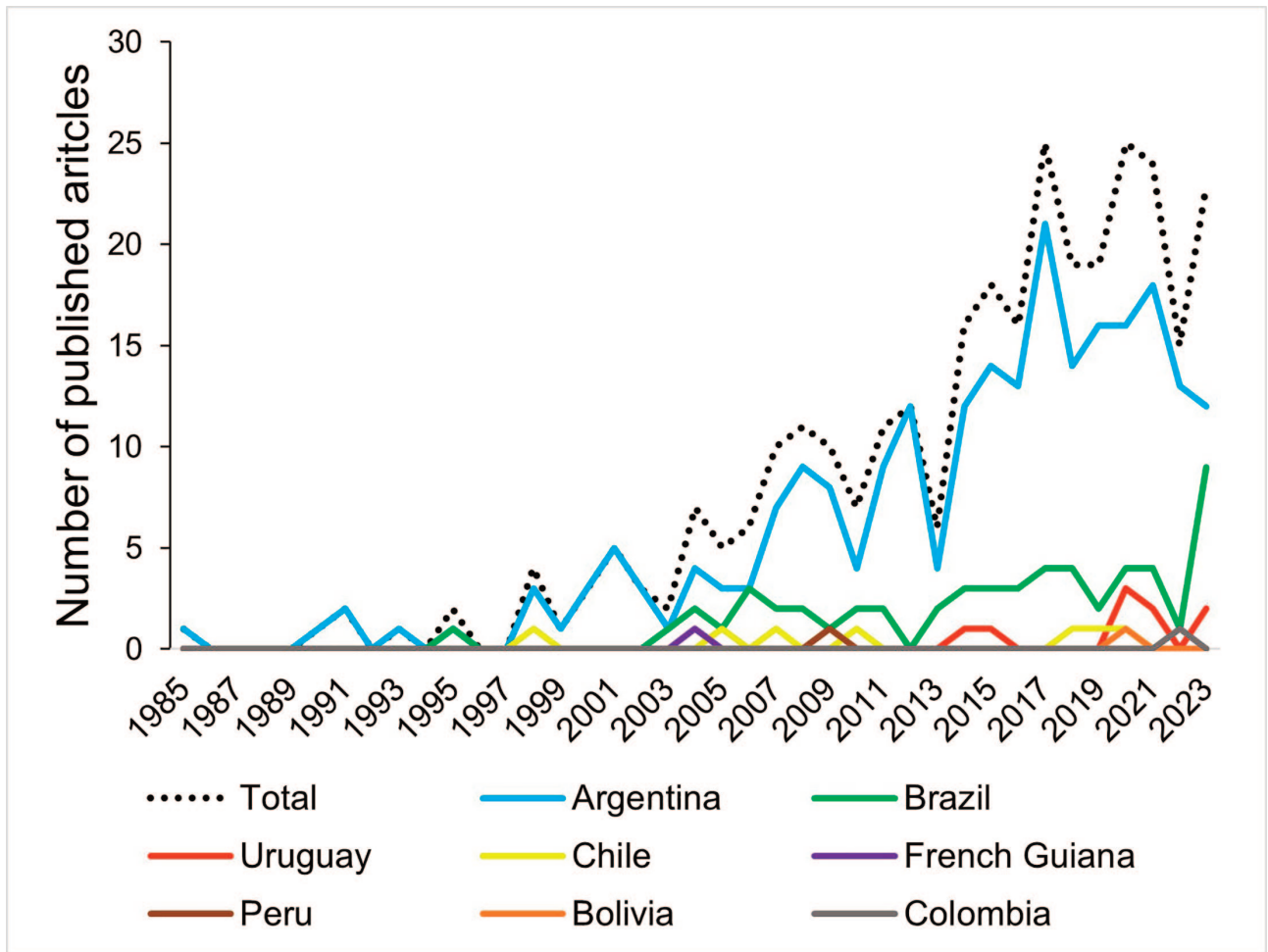


Figure 1. Number of actualistic taphonomy studies published per year from 1985 to 2023, shown by country.

charcoal, pottery, and rock art paintings, remained poorly studied (accounting for 5.9% when considered collectively) (Fig. 8). When examining the geographical distribution of the studies conducted (Fig. 9), it is noteworthy that most indicators have been predominantly studied in Argentina, generally with good regional coverage, except for the less-represented groups. The two dominant indicators (vertebrates and mollusks) showed a differential distribution pattern, with vertebrates mainly represented in terrestrial environments and mollusks in marine environments (Fig. 9). There were a few indicators that showed highly restricted localizations, such as diatoms in the Buenos Aires Province (Argentina) or brachiopods in Ubatuba Bay (Brazil). Others, such as pollen and phytoliths, showed disjunct distributions, with studies concentrated in some regions of Brazil and Argentina.

The dissemination of actualistic taphonomy research in South America has spanned 92 journals (Fig. 10) and 28 book chapters. Among them, *Palaios* stands out as the journal with the highest number of published studies (8.2%), followed by *Quaternary International* (6.4%) and the archaeological journal *Intersecciones en Antropología* (5.0%). Notably, 72.2% of South American actualistic taphonomy papers published in *Quaternary International* correspond to archaeological research (Suppl. Inf. 1). Indeed, a higher percentage (40.5%) of the total articles surveyed have been published in archaeological journals (i.e., *Journal of Archaeological Science*, *Archaeofauna*, *Archaeological*, and *Anthropological Sciences*, among others). Regarding language, most publications (69.7%) were written in English, followed by 29.7% in Spanish, and only 0.6% in Portuguese (Suppl. Inf. 1).

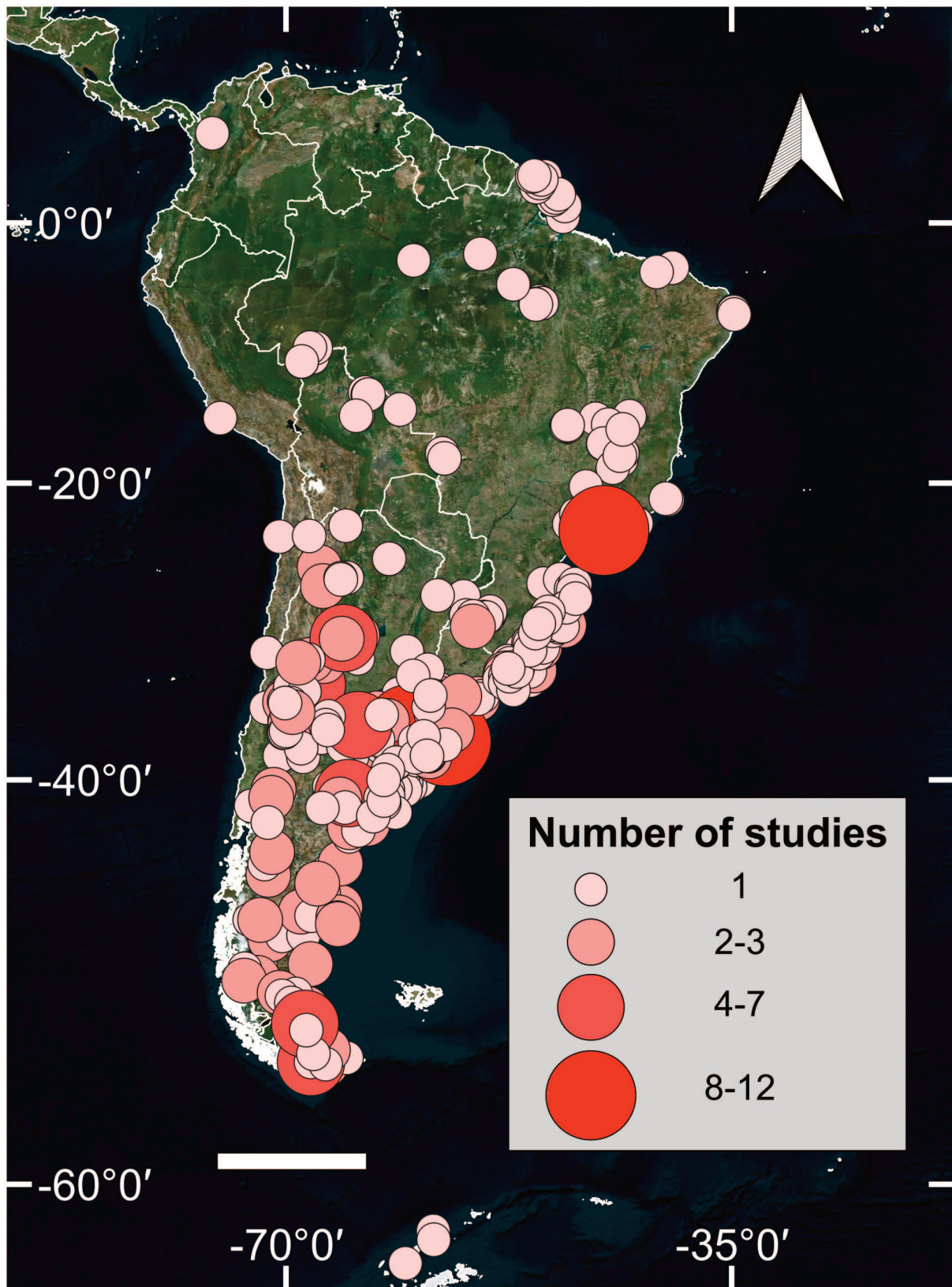


Figure 2. Map of South America showing the frequency of actualistic taphonomy studies conducted in different areas. Scale bar= 1000 km. (Satellite image Bing, QGIS, accessed July 2025).

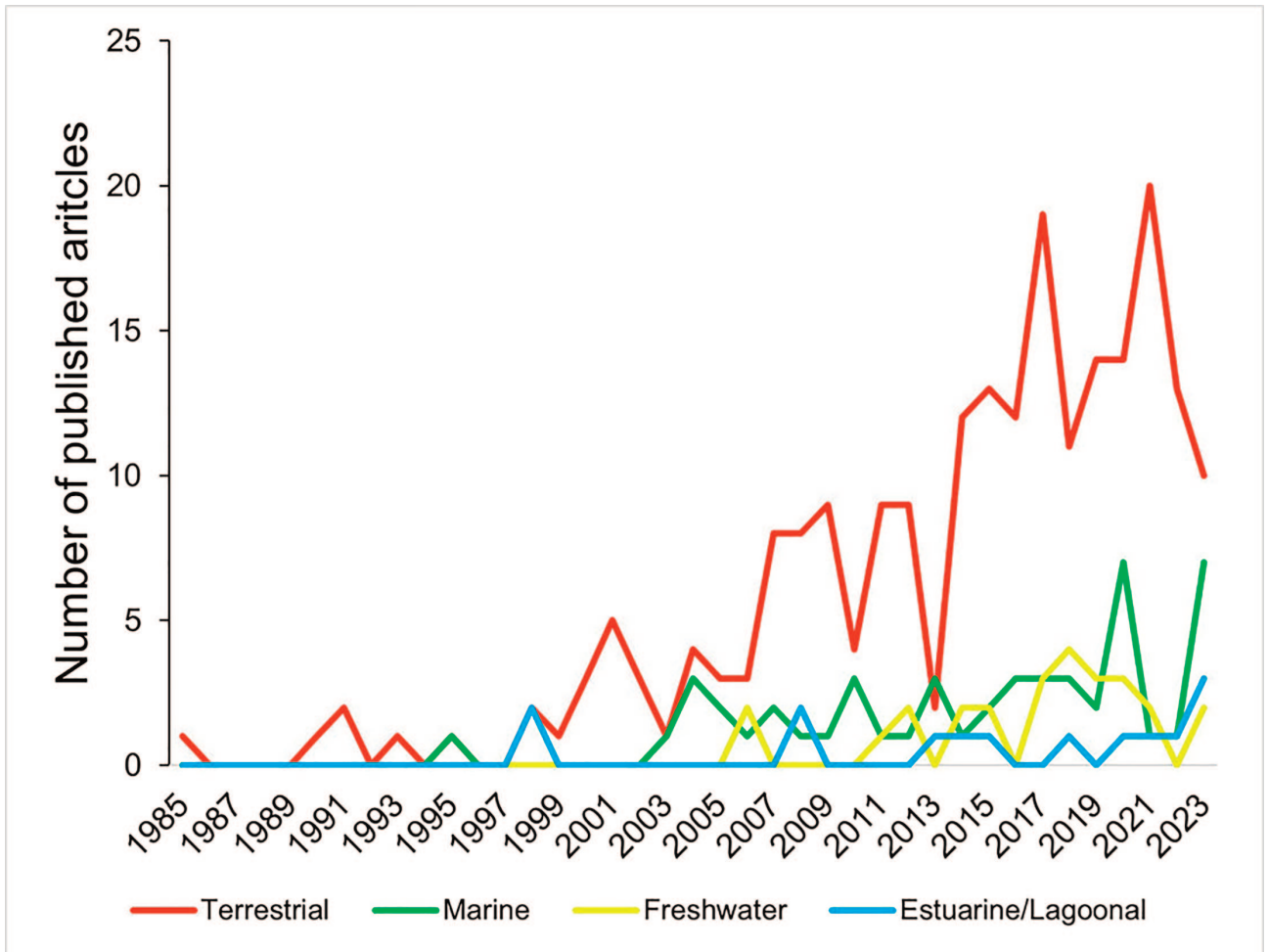


Figure 3. Number of actualistic taphonomy studies published per year from 1985 to 2023, categorized by environment type (marine, estuarine/lagoonal, freshwater, terrestrial).

DISCUSSION

Our results revealed a steady increase in actualistic taphonomy studies in South America from 1985, with Argentina leading this trend, followed by Brazil and Uruguay. However, this might be attributed to a stronger archaeological and paleontological tradition in these countries, although alternative explanations, such as more opportunities for funding availability or institutional support, cannot be ruled out. Argentina's prominence in these studies could be linked to several factors, such as the country's primary development of a strong academic archaeology, the theoretical influence of North American archaeology, abundant research in hunter-gatherer archaeology, and the early growth of zooarchaeology. In fact, the first actualistic taphonomy article in our database was a study aimed at addressing an

archaeological question involving a two-year monitoring of guanaco skeletons in Tierra del Fuego, Patagonia, Argentina (Borrero, 1985). Since then, actualistic taphonomy studies rapidly expanded to mammalian carnivores, mostly in southwestern Patagonia and, to a lesser extent, southern Puna (Mondini & Muñoz, 2008). In the Pampas region, studies began later, towards the late 1990s and early 2000s (Gutiérrez *et al.*, 2018). In Brazil, unlike in Argentina, the rise of actualistic taphonomy began in 2003 with studies conducted in marginal marine environments, primarily focusing on subtidal accumulations of terebratulid brachiopods and, more recently, on mollusks. These studies played a key role in establishing the field and provided valuable insights into taphonomic processes in these settings (Simões *et al.*, 2009), especially concerning time-averaging estimates

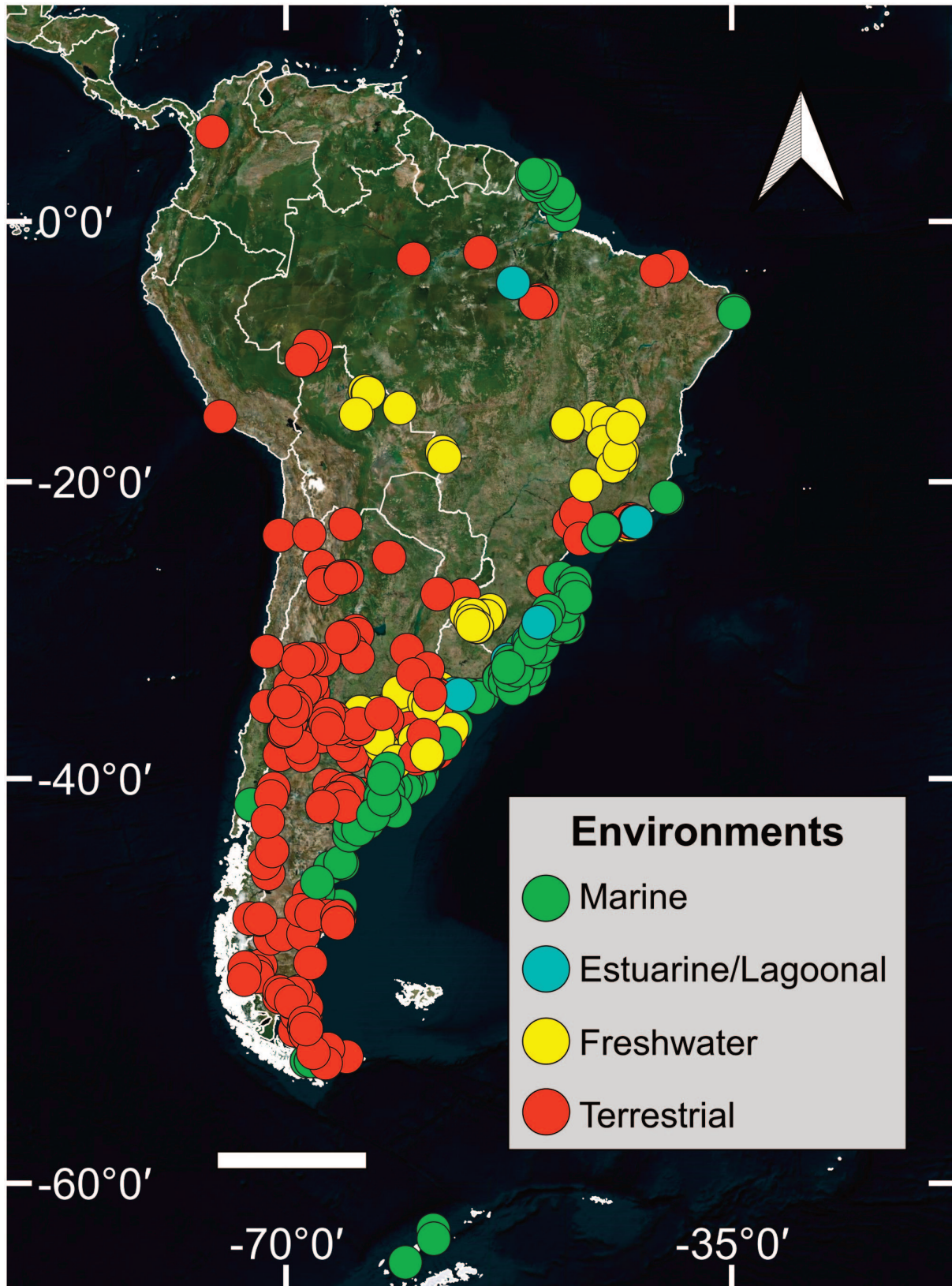


Figure 4. Map of South America showing the locations of all actualistic taphonomy study sites, differentiated by environment type (marine, estuarine/lagoonal, freshwater, terrestrial). Scale bar= 1000 km. (Satellite image Bing, QGIS, accessed July 2025).

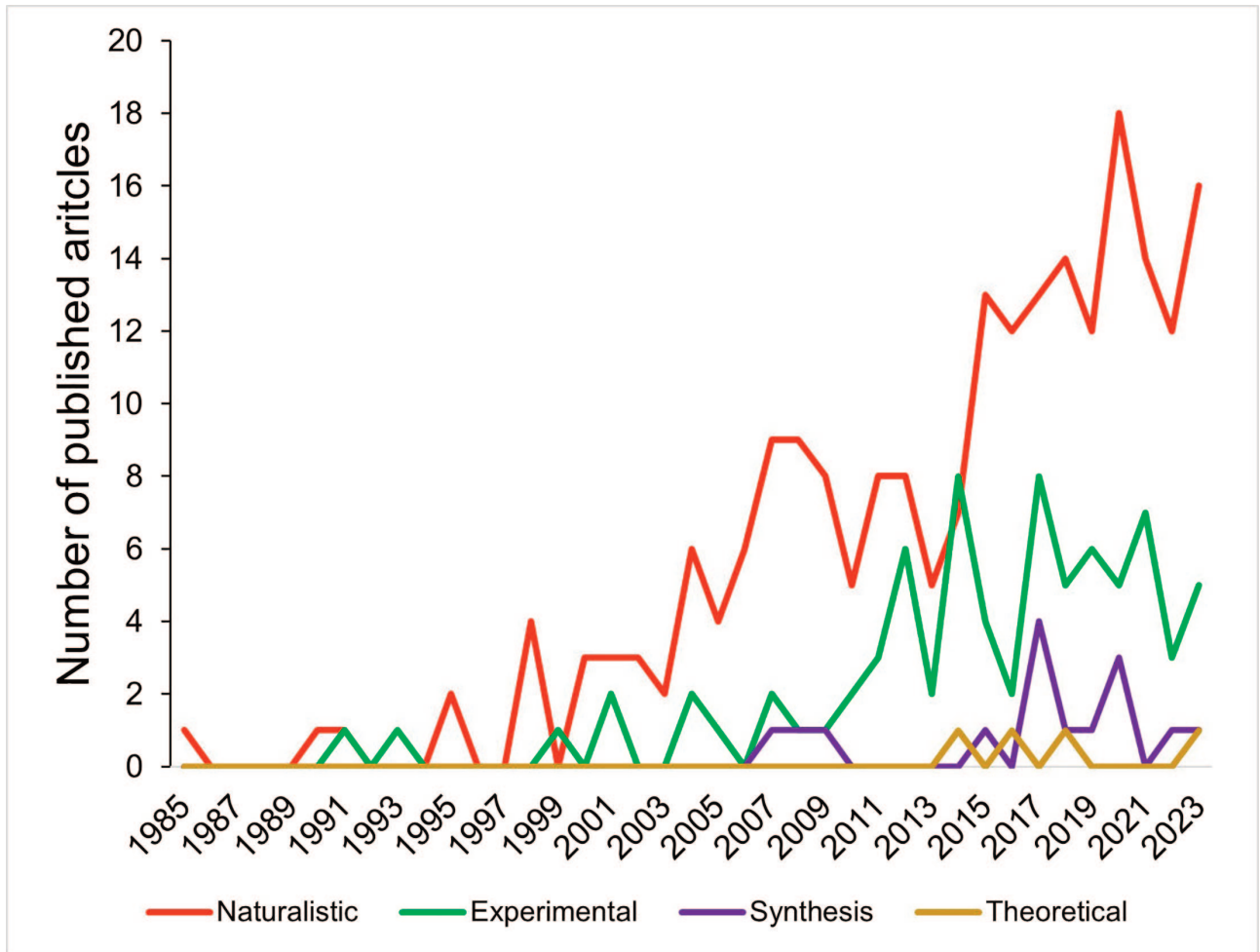


Figure 5. Number of actualistic taphonomy studies published per year from 1985 to 2023, categorized by study type (naturalistic, experimental, synthesis, theoretical).

(e.g., Carrol *et al.*, 2003; Dexter *et al.*, 2014; Ritter *et al.*, 2017, 2023b; Krause *et al.*, 2010; see Suppl. Inf. 1 for a complete list). The first studies conducted in Uruguay were related to archaeological shell middens, aiming to identify differences between natural and anthropogenic mollusk accumulations (e.g., Beovide & Martínez, 2014). Over time, actualistic taphonomy studies began to develop with paleontological objectives, primarily focusing on marine mollusks (Rojas & Martínez, 2020). This disciplinary divide highlights a significant bias in South American actualistic taphonomy: archaeological studies have primarily focused on terrestrial environments and vertebrates, whereas paleontological research has largely been restricted to marine mollusks. Bias in archaeological research primarily results from disciplinary scope, as it focuses on the sphere of human activity

and the materials represented in the archaeological record. This specialization limits a broader understanding of taphonomic processes across diverse settings.

Environments. The dominance of terrestrial environments in actualistic taphonomic research (70.8%) is primarily driven by the contributions of archaeologists and vertebrate paleontologists. This strong focus likely reflects both the accessibility of terrestrial sites and a historical emphasis on understanding fossilization processes in vertebrate remains and archaeological contexts. However, this bias constrains insights into taphonomic dynamics in other environments. Despite their extensive fossil record, marine settings account for only 16.2% of studies, with estuarine and lagoonal environments even less represented. Logistical challenges in conducting long-term coastal observations

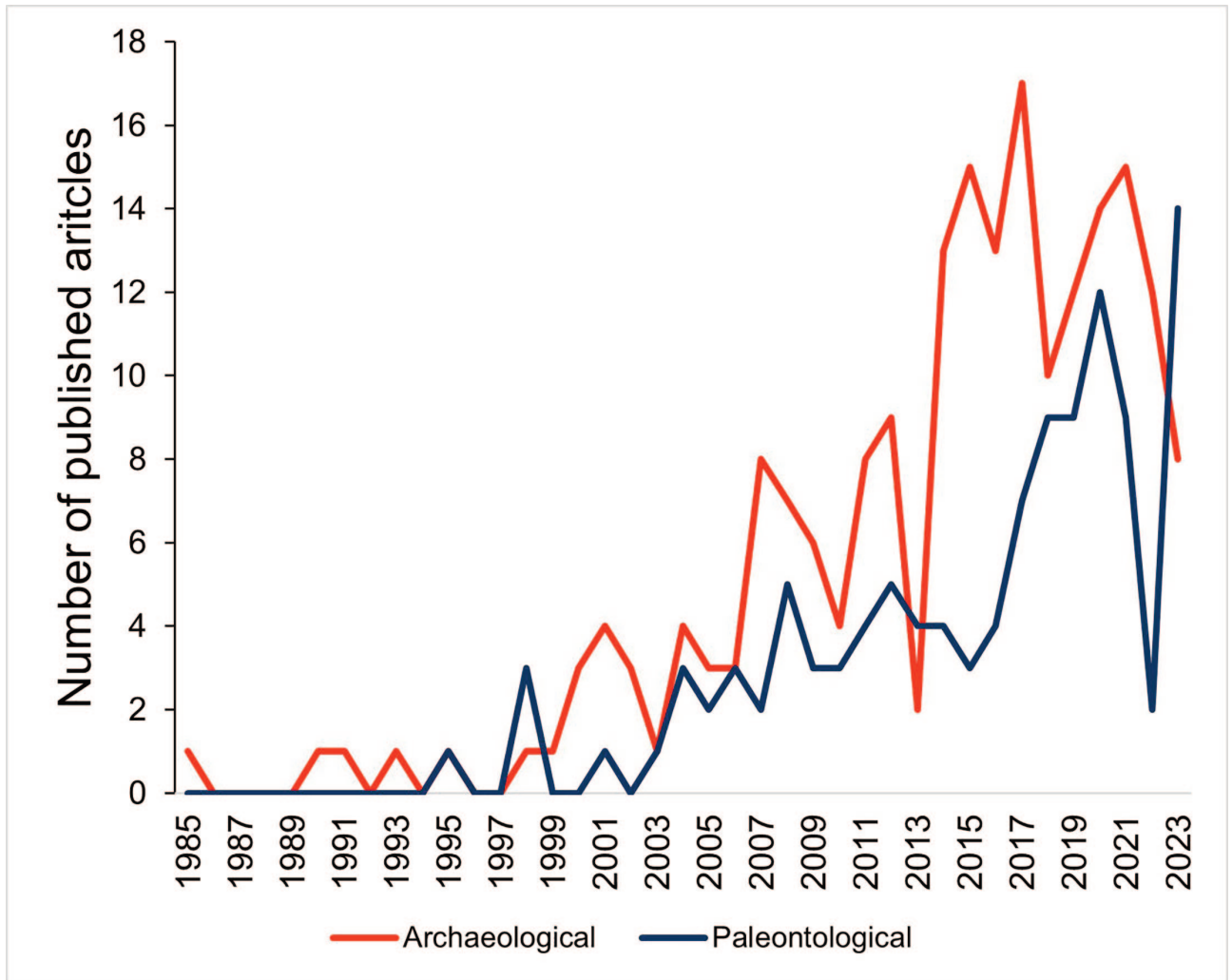


Figure 6. Number of actualistic taphonomy studies published per year from 1985 to 2023, categorized by research objective (archaeological or paleontological).

may contribute to this imbalance. Since 2006, freshwater actualistic taphonomy has gained traction (8.4%), indicating a growing interest in depositional and post-mortem processes in riverine and lacustrine systems (e.g., Erthal *et al.*, 2011; De Francesco *et al.*, 2020; Hassan *et al.*, 2020; see Suppl. Inf. 1 for a complete list), though its representation remains low compared to terrestrial studies. Moreover, geographic disparities exist, with marine and estuarine studies concentrated along the Atlantic coast. Meanwhile, actualistic taphonomy along the Pacific, especially in Chile, has developed differently, underscoring the need for expanded research in underrepresented coastal regions. The geological difference between the relatively stable Atlantic coast and Chile's tectonically active Pacific coast may have

shaped the divergent development of actualistic taphonomy in these regions.

Study type and disciplinary focus. The predominance of field-based naturalistic research (68.4%) reflects the discipline's foundational emphasis on observing taphonomic processes *in situ*. Studies on taphonomic patterns, taphofacies, live-dead fidelity, and time-averaging have been pivotal. Experimental studies, initiated in 1991, increased markedly after 2009, likely due to technological advancements and interdisciplinary collaborations enabling more refined methodologies. The emergence of synthesis studies in 2007 suggests a maturation of the field, where comprehensive reviews and meta-analyses became possible. These studies likely played a crucial role in integrating diverse

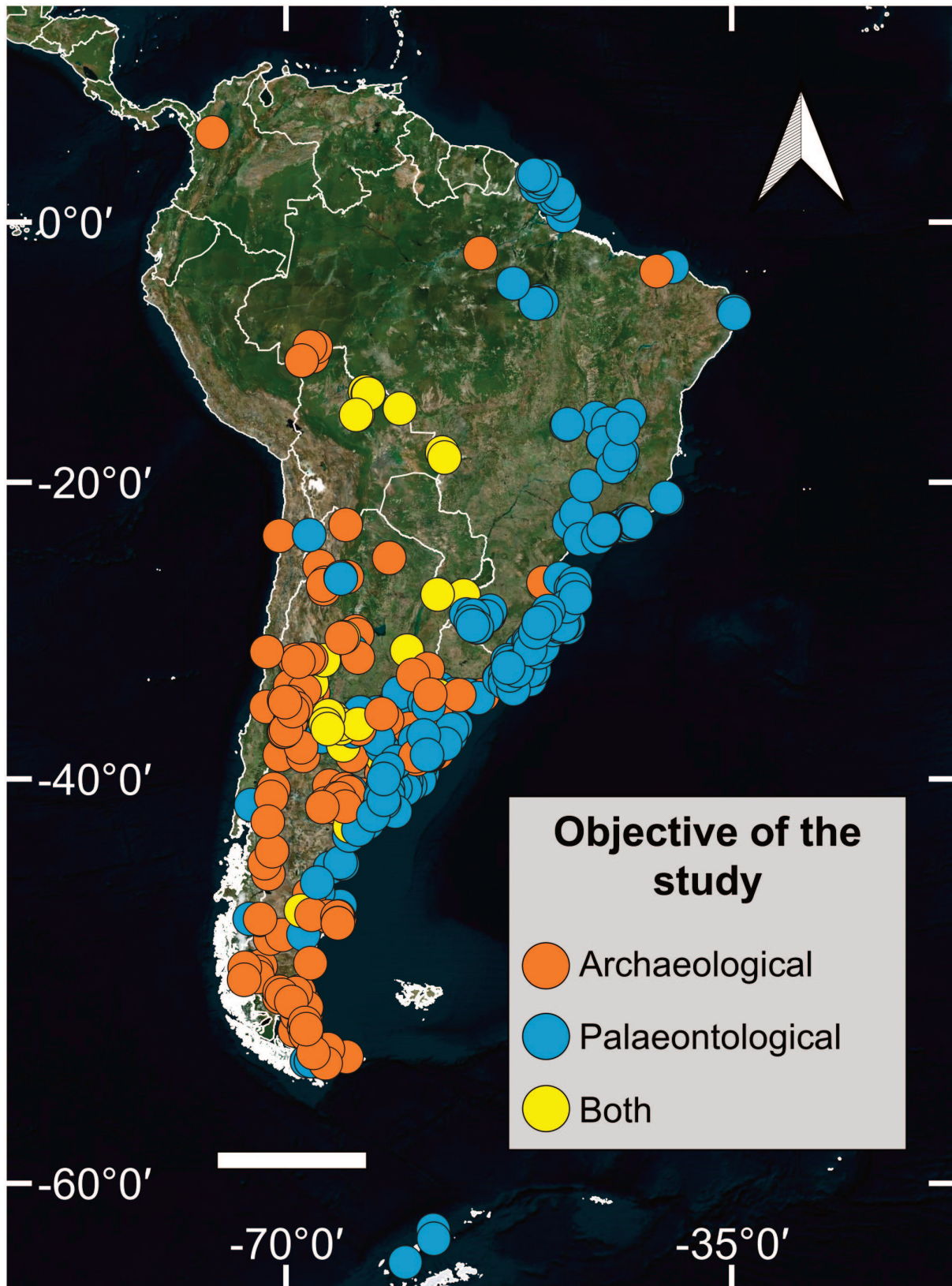


Figure 7. Map of South America showing the locations of all actualistic taphonomy study sites, differentiated by research objective (archaeological or paleontological). Scale bar= 1000 km. (Satellite image Bing, QGIS, accessed July 2025).

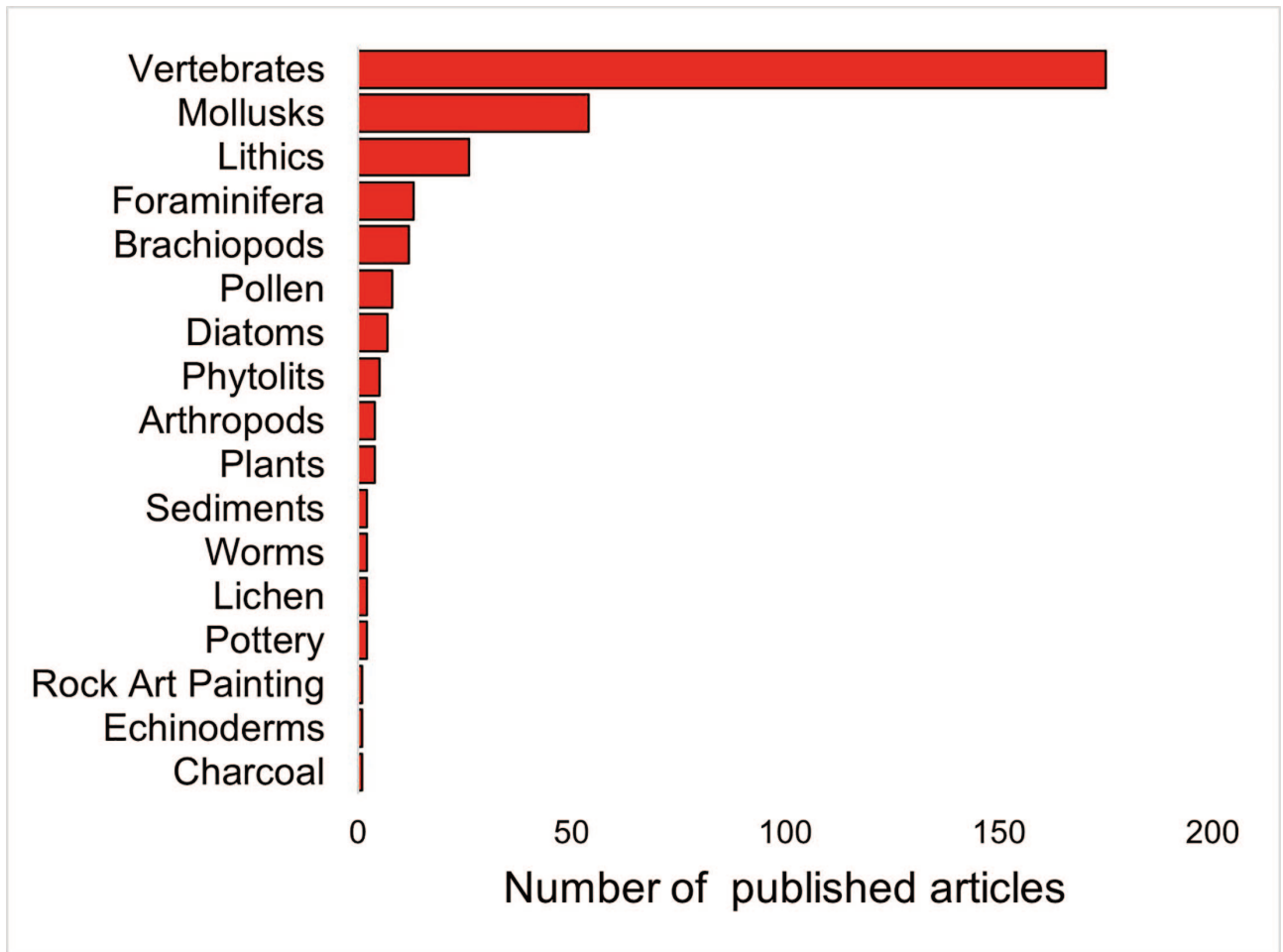


Figure 8. Total number of actualistic taphonomy studies published for each type of taphonomic indicator.

lines of evidence, identifying research gaps, and setting new directions for actualistic taphonomy. The rise of theoretical studies since 2016 indicates a conceptual shift, emphasizing broader frameworks for interpreting taphonomic data.

Archaeological applications have played a pioneering role in shaping South American actualistic taphonomy. Taphonomic analyses have been crucial in distinguishing natural from anthropogenic accumulation processes, improving the explanations of the patterns exhibited by the archaeological record, and reinforcing the field's deep integration with archaeology. In contrast, paleontological applications grew rapidly after 2015, reflecting an increasing interest in applying taphonomic principles to the fossil record. This shift likely results from new research questions, methodological advancements, and a growing recognition of taphonomy's relevance in paleoecology and

evolutionary studies.

Taphonomic indicators. Vertebrates dominate actualistic taphonomic studies due to their central role in archaeology and paleontology. The extensive vertebrate fossil record and its significance in reconstructing past environments and human-animal interactions reinforce its prominence. Similarly, the significant presence of lithics underscores the relevance of stone artifact taphonomy in archaeological research, where identifying natural and anthropogenic modifications is essential (Borrazzo, 2016). Mollusks, primarily from marine contexts, rank second, highlighting their importance in studies of shell accumulations, live-dead fidelity, and environmental reconstructions. While vertebrates and mollusks are well represented, other indicators, such as foraminifera, brachiopods, pollen, diatoms, and phytoliths, remain understudied. Even less

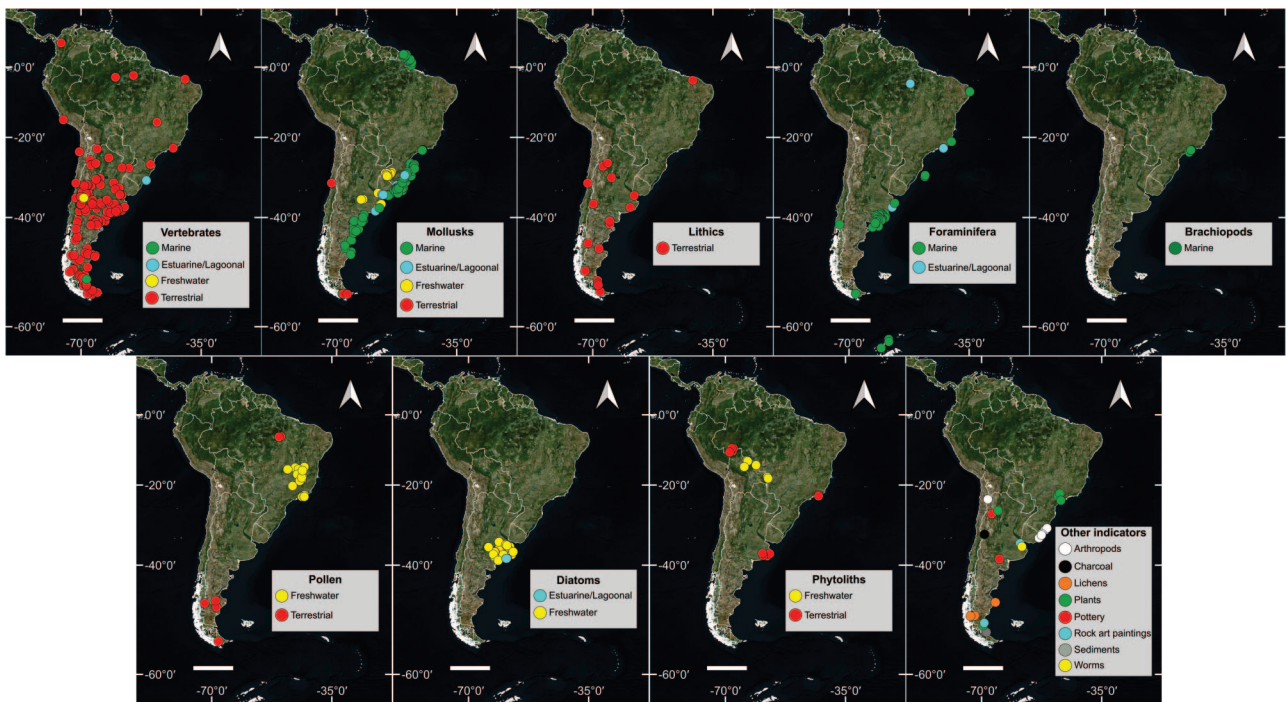


Figure 9. Composite map of South America showing the geographical distribution of each taphonomic indicator. Each panel displays the sites where a given indicator was studied, differentiated by environment type (marine, estuarine, freshwater, terrestrial). Scale bar= 1000 km. (Satellite image Bing, QGIS, accessed July 2025).

explored are plants, arthropods, lichens, worms, sediments, echinoderms, charcoal, pottery, and rock art paintings. These indicators are critical for paleoenvironmental reconstructions, human land use studies, and refining chronological frameworks. Yet, their limited representation suggests that actualistic taphonomy has not fully incorporated a broader range of materials, potentially overlooking key processes affecting different substrates.

Publications. The interdisciplinary nature of South American actualistic taphonomy is evident in its dissemination across 92 journals. The prominence of *Palaïos* as the leading publication venue underscores its historical role in shaping taphonomic research, particularly in moving beyond Efremov's (1940) initial framework, which focused on fossil record incompleteness, toward recognizing taphonomic signatures as paleoenvironmental tools (Parsons-Hubbard *et al.*, 2011). *Palaïos* was established in 1986, which not only coincides with the emergence of actualistic taphonomy in South America but also suggests that the continent was actively engaging with the broader global movement in this field. The presence of *Quaternary International* as the second

most common outlet highlights the relevance of actualistic taphonomy in Quaternary studies, particularly in understanding recent paleoenvironmental changes. Similarly, the significant representation of *Intersecciones en Antropología* reinforces the strong connection between taphonomic research and archaeology in Argentina. Notably, 40.5% of articles are published in archaeological journals, underscoring the discipline's integration with archaeology, particularly in identifying the imprint of natural and anthropogenic processes on the archaeological record. However, the lower representation of taphonomic research in strict paleontological journals suggests that, despite its importance, actualistic taphonomy remains underutilized in mainstream paleontological discourse. Greater incorporation of taphonomic principles into fossil assemblage studies, stratigraphic interpretations, and evolutionary analyses could help bridge this gap and foster a more holistic understanding of past environments. The predominance of English as the publication language (69.7%) further reflects a strong orientation toward international visibility and scholarly integration beyond regional boundaries.

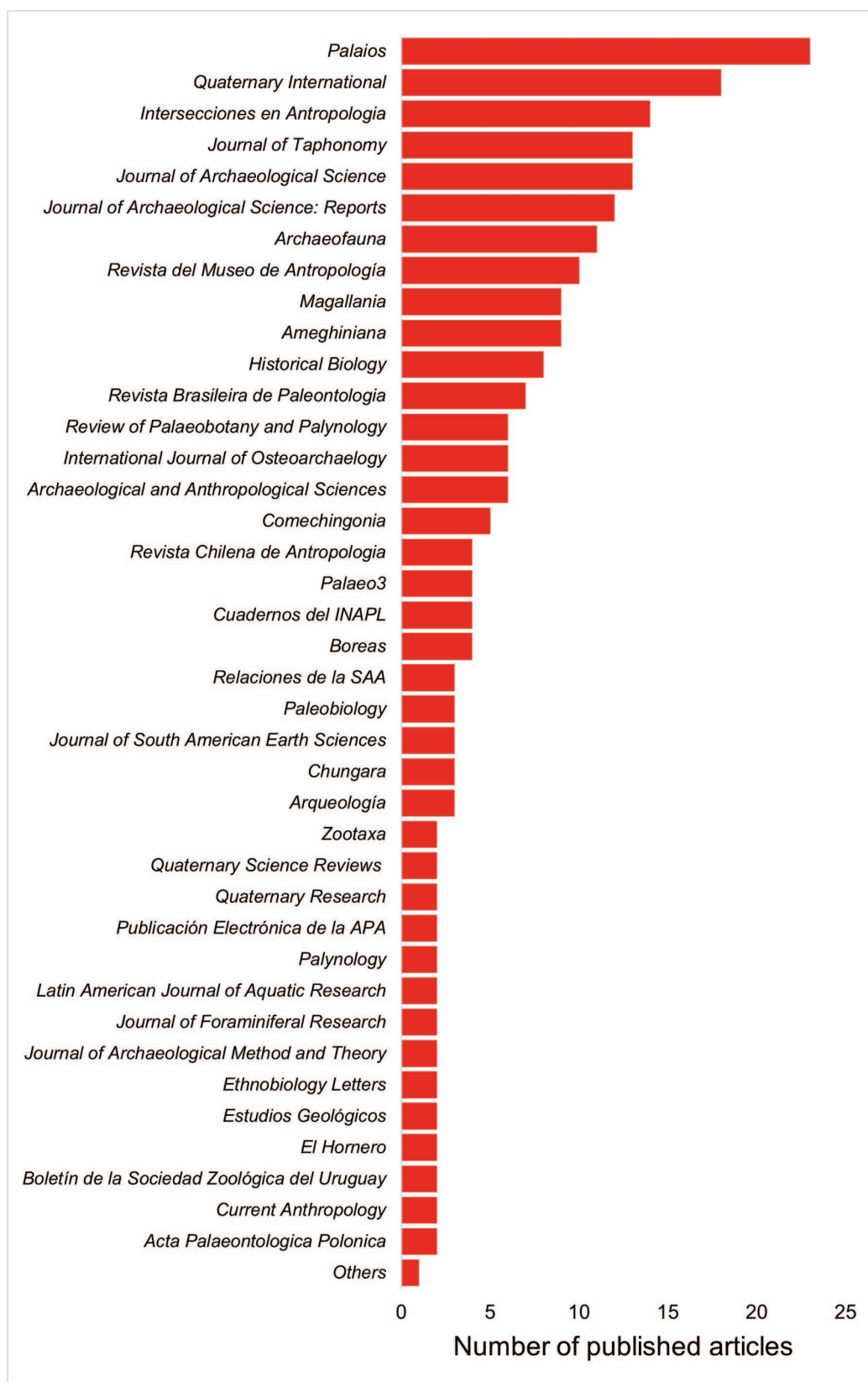


Figure 10. Total number of actualistic taphonomy studies published in each scientific journal.

Limitations and future directions. While this review provides a comprehensive overview of actualistic taphonomy in South America, several methodological and structural limitations must be acknowledged. First, the predominance of publications in English (69.7%), followed by Spanish (29.7%) and Portuguese (0.6%), reflects a language bias that may hinder the visibility and accessibility of research conducted locally. The dominance of English-language journals can create barriers for researchers aiming to publish in their native languages (for a discussion of this idea, see Bortolus, 2012), especially given the limited number of indexed journals in the region specializing in taphonomic or actualistic studies.

Another limitation stems from the dependence on keyword-based searches. Several potentially relevant studies, particularly those dealing with actualistic neoichnology or experimental observations of preservation processes, may not have identified themselves explicitly as “actualistic taphonomy” and were thus not retrieved. This highlights a broader disciplinary challenge: the field remains loosely defined in some contexts, and many researchers conducting relevant work may not use standardized terminology, limiting both discoverability and synthesis efforts.

Regarding publication venues, the concentration of papers in a few key journals—*Palaios*, *Quaternary International*, and *Intersecciones en Antropología*—reveals a narrow publishing landscape. Notably, few papers appear in mainstream paleontological journals, suggesting that actualistic taphonomy is still underrepresented in core paleontological discourse.

Geographically, the field is dominated by contributions from Argentina and Brazil, pointing to regional disparities in infrastructure, research funding, and academic traditions. Studies are often disconnected, with limited continuity or integration across research teams, which hinders the development of sustained, programmatic research lines. Future efforts should focus on strengthening regional collaborations, standardizing terminology, encouraging the inclusion of actualistic taphonomy in a broader array of journals, and expanding the scope of the discipline to include underrepresented areas such as plant taphonomy and neoichnology. Addressing these limitations will enhance the field’s cohesion, visibility, and scientific impact.

CONCLUSION

Considering the patterns identified, we advocate for a coordinated regional agenda to strengthen actualistic taphonomy in South America. This should include the systematic exploration of underrepresented environments (such as estuarine, lagoonal, and tropical systems), the incorporation of neglected taxonomic groups (e.g., plants, arthropods, and microbial communities), and the integration of experimental approaches across diverse ecological contexts. Expanding interdisciplinary collaborations, particularly between archaeology, paleontology, ecology, and conservation sciences, will be key to consolidating the field. Furthermore, establishing open-access databases and long-term monitoring programs can foster comparative studies and meta-analyses, enabling broader insights into taphonomic processes and their paleoenvironmental significance. In this regard, South America has the potential to not only fill global knowledge gaps but also to contribute conceptually to developing a more inclusive and ecologically grounded taphonomy.

ACKNOWLEDGMENTS

We thank Marcello Simões, María Belén Tomaselli, and an anonymous reviewer for their helpful comments that significantly improved the manuscript. KB thanks Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Fondo para la Investigación Científica y Tecnológica de la Agencia Nacional de Promoción de la Investigación, el Desarrollo Tecnológico y la Innovación (FONCyT, Agencia I+D+i, grant PICT2018-02807). GSH and CDF thank Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, PIP00204/23) and Universidad Nacional de Mar del Plata (EXA1219/24). SM thanks CSIC-Universidad de la República, Agencia Nacional de Investigación e Innovación (ANII), and the Programa de Desarrollo de Ciencias Básicas (PEDECIBA). CIM thanks Facultad de Ciencias Exactas y Naturales (UNLPam). MNR thanks the Brazilian National Council for Scientific and Technological Development (CNPq/Brazil) grant (processes 313830/2023-1 and 403547/2024-5) and the *Coordenação de Aperfeiçoamento de Pessoal de Nível Superior* – Brazil (CAPES) – Finance Code 001 (process 88881.004176/2024-01). The co-authors were listed alphabetically except for the first author, who was responsible for leading the study.

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doi: 10.5710/PEAPA.24.07.2025.542

Recibido: 11 de abril de 2025

Aceptado: 24 de julio de 2025

Publicado: 20 de octubre de 2025



TAPHONOMY AND GENESIS OF SHELL LENSES: THE CERRO BANDURRIAS LOCALITY (TIERRA DEL FUEGO, ARGENTINA)

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Abstract. This paper presents the taphonomic and geoarchaeological study of a thin shell lens identified 3.2 km from the coast of San Sebastian Bay on the hilltop of the inland Cerro Bandurrias archaeological locality (Tierra del Fuego Province, Argentina). The biological assemblage of the shell lens comprises marine fauna (bivalves, gastropods, and fish) that may represent the remains of the occasional exploitation of littoral resources by hunter-gatherers. However, since the lack of unequivocal anthropogenic signals, alternative non-anthropogenic hypotheses need to be also assessed. Indeed, the time frame of the shell lens (radiocarbon dated as ~6500 cal. years BP) indicates that the bioclast accumulation occurred during the Middle Holocene marine transgression with a different paleogeography, when the hill was part of a coastal landform (peninsula). The methodological design comprised the combination of different and independent sources of information and the techniques applied to assess competing genetic hypotheses. Based on compositional, taphonomic and sedimentological analyses, our research suggests that the most parsimonious explanation is that hunter-gatherers were the primary agents of bioclast accumulation of the lens. Thus, this ephemeral archaeological evidence provides a new record for the human exploitation of littoral resources on the Atlantic coast of Isla Grande de Tierra del Fuego during the Middle Holocene. The conspicuous character of shells improves the archaeological visibility of short term, non-redundant past human occupations.

Key words. Archaeomalacology. Geoarchaeology. Actualistic taphonomy. Hunter-gatherers. Middle Holocene marine transgression. Coastal evolution. Littoral human occupations. Ephemeral archaeological record.

Resumen. TAFONOMÍA Y GÉNESIS DE LENTES DE VALVAS: LA LOCALIDAD CERRO BANDURRIAS (TIERRA DEL FUEGO, ARGENTINA). Este trabajo presenta el estudio tafonómico y geoarqueológico de una lente de valvas identificada a 3,2 km de la costa de la bahía San Sebastián en la cumbre de la localidad arqueológica Cerro Bandurrias (provincia de Tierra del Fuego, Argentina). El conjunto biológico está compuesto por fauna marina (bivalvos, gasterópodos y peces) y fue interpretado como los restos materiales de la explotación ocasional de recursos litorales realizada por cazadores-recolectores. Sin embargo, la ausencia de evidencia de origen antrópico inequívoca hizo necesario evaluar hipótesis alternativas que propongan una génesis no antrópica. El marco temporal dado por un fechado radiocarbónico de ~6500 años cal. AP indica que la acumulación de bioclastos ocurrió durante la Transgresión Marina del Holoceno medio con una paleogeografía diferente, cuando el cerro era parte de una geoforma costera (península). Aquí presentamos el diseño metodológico, que incluye una combinación de fuentes de información distintas e independientes para evaluar las hipótesis en competencia. En base a los análisis composicionales, tafonómicos y sedimentológicos, nuestra investigación sugiere que la explicación más parsimoniosa es que los cazadores-recolectores fueron los agentes principales de acumulación en la lente. Por lo tanto, esta evidencia arqueológica efímera provee un nuevo registro para la explotación humana de recursos litorales en la costa atlántica de la Isla Grande de Tierra del Fuego durante el Holoceno medio. El carácter conspicuo de las valvas aumenta la visibilidad arqueológica de ocupaciones humanas breves y no redundantes.

Palabras clave. Arqueomalacología. Geoarqueología. Tafonomía actualista. Cazadores-recolectores. Transgresión marina del Holoceno medio. Evolución costera. Ocupaciones humanas litorales. Registro arqueológico efímero.

SHELL MOUNDS, beds, and lenses are widespread features of the fossil record. Several taphonomic and archaeological models based on contemporary observations and ancient

deposits have been developed to explain the genesis of these bioclastic concentrations (e.g., Meehan, 1975; Claassen, 1991, 2000; Kidwell & Holland, 1991; Stein, 1992;

Kowalewski *et al.*, 1994; Orquera & Piana, 2000, 2001; Kowalewski & LaBarbera, 2004; Favier Dubois & Borella, 2007; Briz Godino *et al.*, 2011; Hammond, 2015; Zangrando *et al.*, 2020; Gomes Rodrigues *et al.*, 2024). Depending on their origin, the study of marine shell-rich deposits may provide information about ocean life and ecosystems, landscape evolution and environmental change, or insights into past human-sea relationships (*e.g.*, Martínez *et al.*, 2006; Zanchetta *et al.*, 2012; Bjerk *et al.*, 2016). Therefore, once these deposits are identified, methodological tools are applied to describe and interpret the meaning of shell accumulations according to disciplinary goals and interests (*e.g.*, Meldahl, 1993; Claasen, 1998; Kowalewski, 2002). Regardless of the field of study, taphonomy proved to be key to critically assessing the pool of agents and processes involved in shell accumulation (*e.g.*, Kidwell *et al.*, 1986; Kidwell & Holland, 1991; Gutiérrez Zugasti, 2008–2009; Hammond, 2014; Beovide & Martínez, 2020).

However, there are cases in which the natural or cultural genesis of shell accumulation is not self-evident. Hence, these ambiguous deposits pose a crossroads for paleontological, geological, and archaeological research that requires further assessment (*e.g.*, Attenbrow, 1992; Henderson *et al.*, 2002; Beovide *et al.*, 2015). Among the elements that have been used for distinguishing shell middens from shell beds are stratigraphic, compositional (*e.g.*, taxonomic diversity and specimen size), and taphonomic characteristics (*e.g.*, Attenbrow, 1992; Henderson *et al.*, 2002; Beovide *et al.*, 2015). In addition, the thermal alteration of shells is a feature exhibited by archaeological deposits but not recorded in natural shell accumulations (Beovide *et al.*, 2015), although ethnography and archaeological experimental studies showed that shells may not always develop and preserve perceptible changes after cooking (*e.g.*, Meehan, 1975; Villagrán, 2014). Moreover, the presence of artifacts (*i.e.*, human-made objects, such as stone tools or pottery) and/or natural elements (*e.g.*, bones, shell, and wood) that exhibit cultural modifications (*e.g.*, cut marks, spiral fractures, flake scars, and thermal alteration) is considered a diacritical mark for anthropogenic shell accumulations. These cultural shell-rich deposits range in South America from large mounds (such as those of the *sambaquis*; Wagner *et al.*, 2011) through shell middens to thin shell lenses (Zangrando, 2020).

In this paper, we study the origin of thin shell lenses in the north of Isla Grande de Tierra del Fuego (IGTDF) that are spatially associated with the Atlantic shoreline position during the Middle Holocene marine transgression. The regional archaeological background indicates that hunter-gatherer populations inhabited northern Isla Grande since the end of the Pleistocene (Massone, 1987, 2004), but the exploitation of marine resources is only recorded from the Middle Holocene onwards (*e.g.*, Salemme & Bujalesky, 2000; Salemme *et al.*, 2014; Santiago, 2024). Here, we present the multidisciplinary study of a thin shell lens recently exposed by aeolian erosion at the summit of Cerro Bandurrias, a hill located in the south of San Sebastian Bay (Fig. 1.1–2). We describe the deposit (geometry and stratigraphic pedolithological units), characterize its biogenic content and chronology to evaluate different hypotheses for the origin of the Cerro Bandurrias lens that consider geogenic, biogenic, and anthropogenic processes.

GEOLOGICAL AND ARCHAEOLOGICAL BACKGROUND

The north of IGTDF represents the southern extreme of the Magellanic steppe, characterized by a cold-temperate oceanic grassland. The mean annual rainfall is ~350 mm and the mean annual temperature is ~5 °C. The strong and frequent wind from the west/southwest quadrant is the most prominent geomorphic agent of the Fuegian steppe (Garreaud *et al.*, 2009; Coronato *et al.*, 2022).

The Cerro Bandurrias is a low (18 masl) and flat-top hill. As the other hills in the south of San Sebastian Bay, it is a small (470 by 280 m) lithic sandstone outcrop of the Carmen Sylva Formation, dated to the Early to Middle Miocene (Codignotto & Malumián, 1981). Edaphized sediments cover the bedrock on the hilltop. The Cerro Bandurrias is currently located 3.2 km from the mean high tide line, but it stood as the northern extreme of a peninsula surrounded by the sea during the Middle Holocene marine transgression (Codignotto, 1983; Isla *et al.*, 1991; Ferrero, 1996; Vilas *et al.*, 1999; Favier Dubois & Borrero, 2005). The maximum transgression occurred between 8500 and 6000 cal. years BP (Candel *et al.*, 2020; Coronato *et al.*, 2022), and the regressive sequence might have begun by *ca.* 5600 cal. years BP (Vilas *et al.*, 1999). The action of marine waves formed cliffs at Cerro Bandurrias foothills. Upon sea retreat,

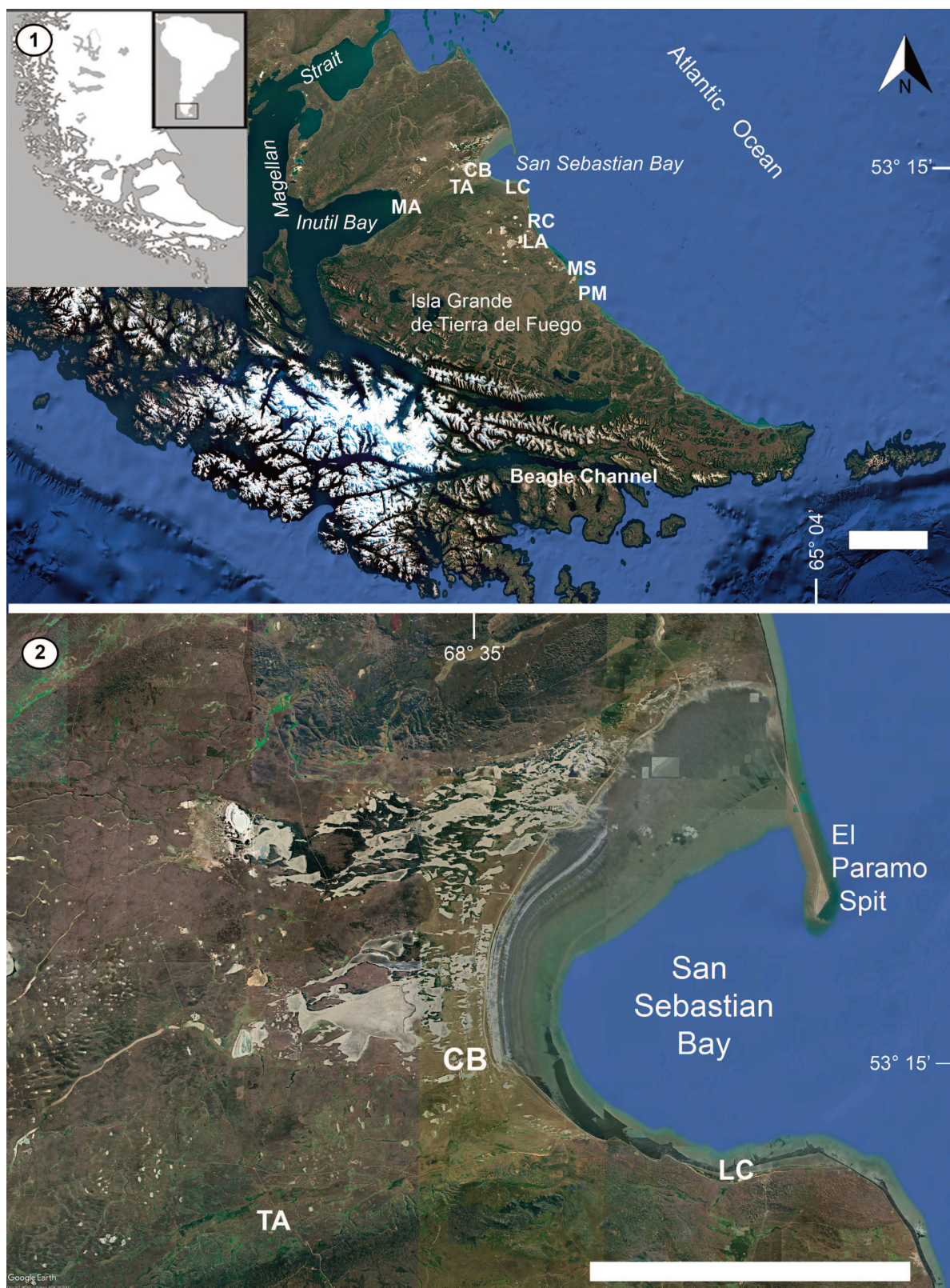


Figure 1. Study region and archaeological contexts mentioned in the text. 1, Isla Grande de Tierra del Fuego. Scale bar= 50 km. 2, San Sebastián Bay. Scale bar= 20 km. References: CB, Cerro Bandurrias; LA, La Arcillosa; LC, Los Chorrillos; MA, Marazzi; MS, Margen Sur; PM, Punta María; RC, Rio Chico; TA, Tres Arroyos. (Image from Landsat/Copernicus 2020; Google Earth, accessed March 2025).

cliff erosion initiated the talus formation at the base of the scarp. San Sebastian Bay evolved with the sea level drop roughly recorded between 5600 and 500 years ago (Fig. 2.1–3). Marshes developed on the emerged plain and grew far from the dominance of the tides (Isla *et al.*, 1991; Vilas *et al.*, 1999; Isla & Bujalesky, 2008; Fig. 2.4). As a result, while the vegetation on Cerro Bandurrias and the other hills includes *Festuca gracillima*, *Poa* sp., and a few specimens of *Berberis* sp., the surrounding plain is occupied by salt grasslands and marshes of *Sarcocornia magellanica* and *Puccinellia* sp. (Bianciotto, 2006). In fact, San Sebastian Bay is the most hypersaline coast of IGDTF mainly due to the existence of extraordinary extensive tidal flats, which in turn, promote the development of marshes with shoals

(*restingas*). The bay is bounded to the north by El Páramo, an 18 km-long gravel/sand spit (Isla *et al.*, 1991; Isla & Bujalesky, 2008; Bujalesky & Gonzalez Bonorino, 2015; Borrero & Borrazzo, 2021).

The earliest evidence of human occupations in the IGDTF is dated to the end of the Pleistocene and it was recorded at Tres Arroyos archaeological locality, situated 20 km to the west of Cerro Bandurrias (Massone, 1987, 2004; Fig. 1.1–2). By that time, the island was still connected to the mainland (*i.e.*, continental Patagonia), thus the peopling of IGDTF was made by pedestrian people who inhabited the lands located to the north of the Magellan Strait. Guanaco (*Lama guanicoe*) was the main staple since the early Fuegian occupations.

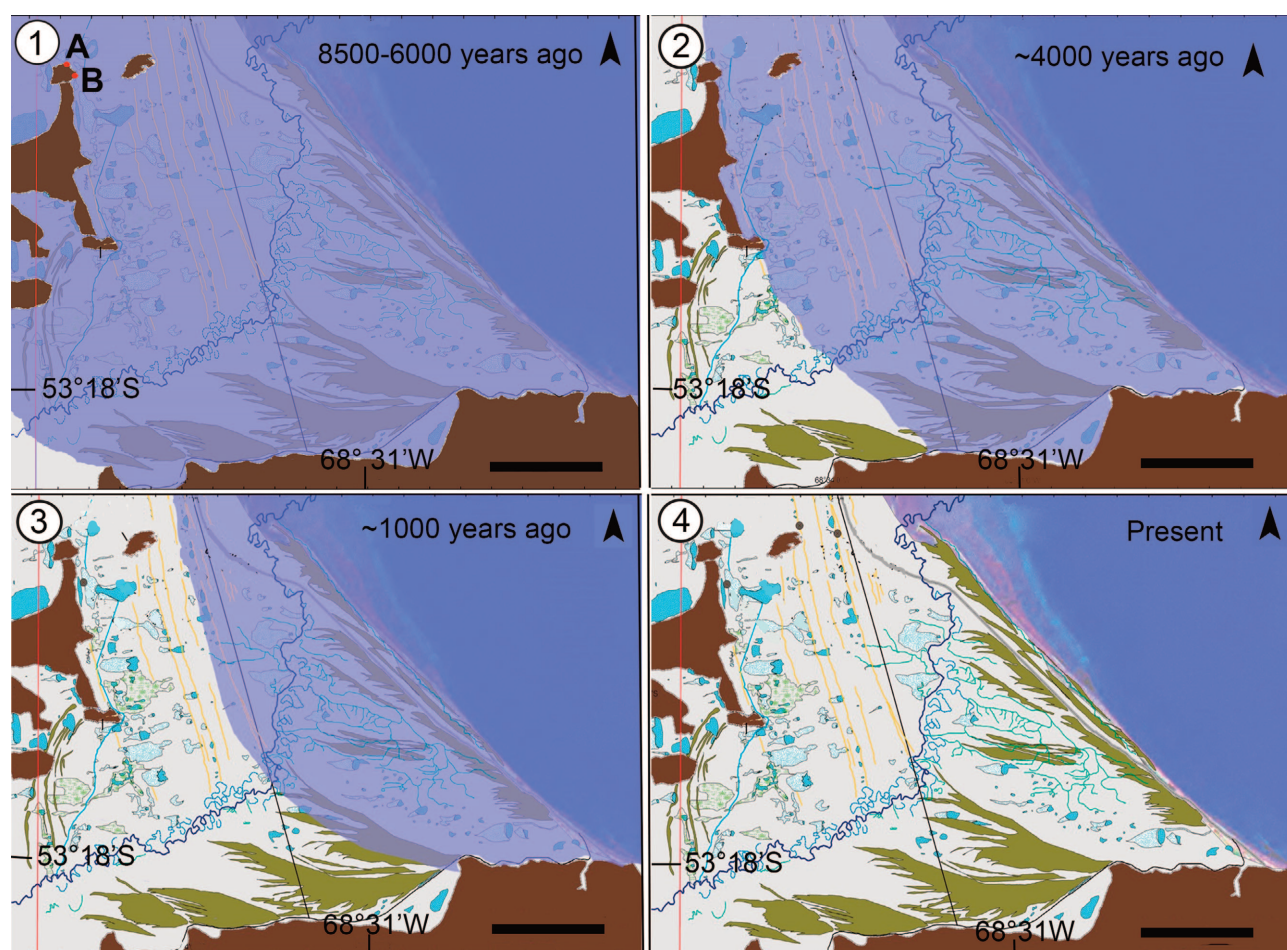


Figure 2. Geomorphological coastal evolution of San Sebastián Bay (based on Vilas *et al.*, 1999; modified from Ozán, 2015). See geomorphological references in Ozán (2015). 1, Estimated position of the coastline 8500–6000 years ago; 2, Estimated position of the coastline *ca.* 4000 years ago; 3, Estimated position of the coastline *ca.* 1000 years ago; 4, Current position of the coastline in the study area. References: A, Location of Cerro Bandurrias shell lens dated by Favier Dubois and Borrero (2005); B, Location of Cerro Bandurrias shell lens studied in this paper. Scale bar= 1 km.

Subsequent archaeological evidence is dated to the Middle Holocene. They include a few sites located near Atlantic coastlines (or paleo coastlines) that exhibit remains of marine fauna (shell, fish, and sea mammals) (Salemme & Santiago, 2017). These Middle Holocene marine records are represented by multicomponent shell middens (*e.g.*, Rio Chico 1, Santiago, 2013; La Arcillosa 2, Salemme *et al.*, 2014), although thin shell lenses composed of *Mytilus* sp. are more common (*e.g.*, La Arcillosa 1 and 3, Salemme & Bujalesky, 2000; Rio Chico 6, Salemme & Santiago, 2017). Among the latter, a small *Mytilus* sp. lens was identified within the sedimentary deposits eroded by the wind in the north of the Cerro Bandurrias summit (located 270 m to the northwest of the locus presented in this paper; Fig. 2.1). These shells were dated to 5700 ± 180 ^{14}C years BP (5199–6096 cal. years BP; Favier Dubois & Borrero, 2005). A stone tool (sidescraper) was recovered at the locus (Borrazzo *et al.*, 2007).

The Late Holocene provides a profuse and diverse record of the human occupation of coastal and inland Fuegian landscapes on the northern Atlantic slope, especially during the last two millennia (Oría *et al.*, 2017). While guanaco remained the primary staple for hunter-gatherers during the Holocene (*e.g.*, Muñoz, 2002; Sierpe, 2020; Santiago, 2024), the exploitation of marine resources introduced during the Middle Holocene became well-established by the Late Holocene.

In sum, two synchronous geomorphological and archaeological processes occurred. Due to littoral accretion, the environment of Cerro Bandurrias turned from marine in the Middle Holocene to inland in the Late Holocene. While this transformation occurred in the landscape, the region was inhabited by hunter-gatherers who increasingly incorporated marine resources into their subsistence since the Middle Holocene.

MATERIALS AND METHODS

A 7 to 10 cm thick shell lens was discovered on the southern hillside of the Cerro Bandurrias in 2022. This feature is observed at 1 m depth, in the sedimentary deposit of the hilltop (Fig. 3.1–3). Horizontally, the shell lens extends discontinuously along 7.47 m in a stratigraphic section exposed by runoff, rotational slides, and wind-

driven scarp retreat. Within this shell-rich level, two segments (2.1 and 0.84 m long) that exhibit a rather continuous distribution of shells along the scarp were identified (Fig. 3.1). These two shell lenses are separated by a 4.53 m long gap, along which only isolated gastropods were identified. Beyond this circumscribed sector of the outcrop, shells were not further observed along the scarp in other deflation hollows placed at the top of the hill.

Considering the thin thickness of the lens, its depth below the surface, its location, orientation, and the risk of lens destruction due to scarp retreat favored by the scarce vegetation, we defined a conservative rescue sampling strategy for our study of the locus. We surveyed the 2.1 m segment by collecting the loose bioclasts available on the surface and further excavating the scarp profile. The 0.84 m segment of the lens was not sampled in order to avoid introducing large-scale modifications on the scarp exposed to westerlies that would promote accelerated and extensive destruction of the context.

During the excavation, it was observed that shells became scarce until they disappeared into the deposit beyond 15 cm from the scarp surface. We recovered the total biological and sedimentary content of the shell-rich layer along the 2.1 m horizontal segment. Although the shells were complete while contained in the sedimentary matrix, they broke during the extraction due to their fragility. To improve the recovery of complete specimens, the lens was excavated by removing blocks of the naturally cemented matrix using a spatula.

Biological components were separated from the matrix at the laboratory. The specimens of the collection (Cerro Bandurrias-Lente de valvas 2022) are housed in the Archaeology Laboratory of the Instituto Multidisciplinario de Historia y Ciencias Humanas. Bioclasts larger than 5 mm were extracted by picking. Smaller bioclasts (corresponding to fragmented shells and fish bones) were separated from sediments by sieving using a 2 mm mesh. A selection of structured blocks of sediments and shells were stored for future studies.

The description of the skeletal concentration follows Kidwell *et al.* (1986) and Kidwell & Holland (1991). The fauna contained in the lens was determined to the lowest possible taxonomic category and its taphonomic attributes

evaluated. Observations of the taphonomic variables of natural and anthropic origin (original color and periostracum preservation, degree of thermal alteration, presence/absence of traces of exfoliation, manganese, cracks, dissolution, abrasion, bioerosion, lichens, root marks, cut marks, anthropic fractures, and decoration) were made macroscopically with the aid of a hand magnifying glass (2.5x) and a stereomicroscope (50x). We followed the

methodological guidelines defined by Hammond (2015) and Gutiérrez Zugasti (2008–2009) for malacological specimens and by Lyman (2008) for vertebrate remains.

Geoarchaeological analyses comprised a detailed stratigraphic characterization of pedolithological units exposed in the section, interpreted within their geomorphological context. Classification followed standardized soil horizon nomenclature (*e.g.*, A, C, R horizons; Birkeland, 1999). The

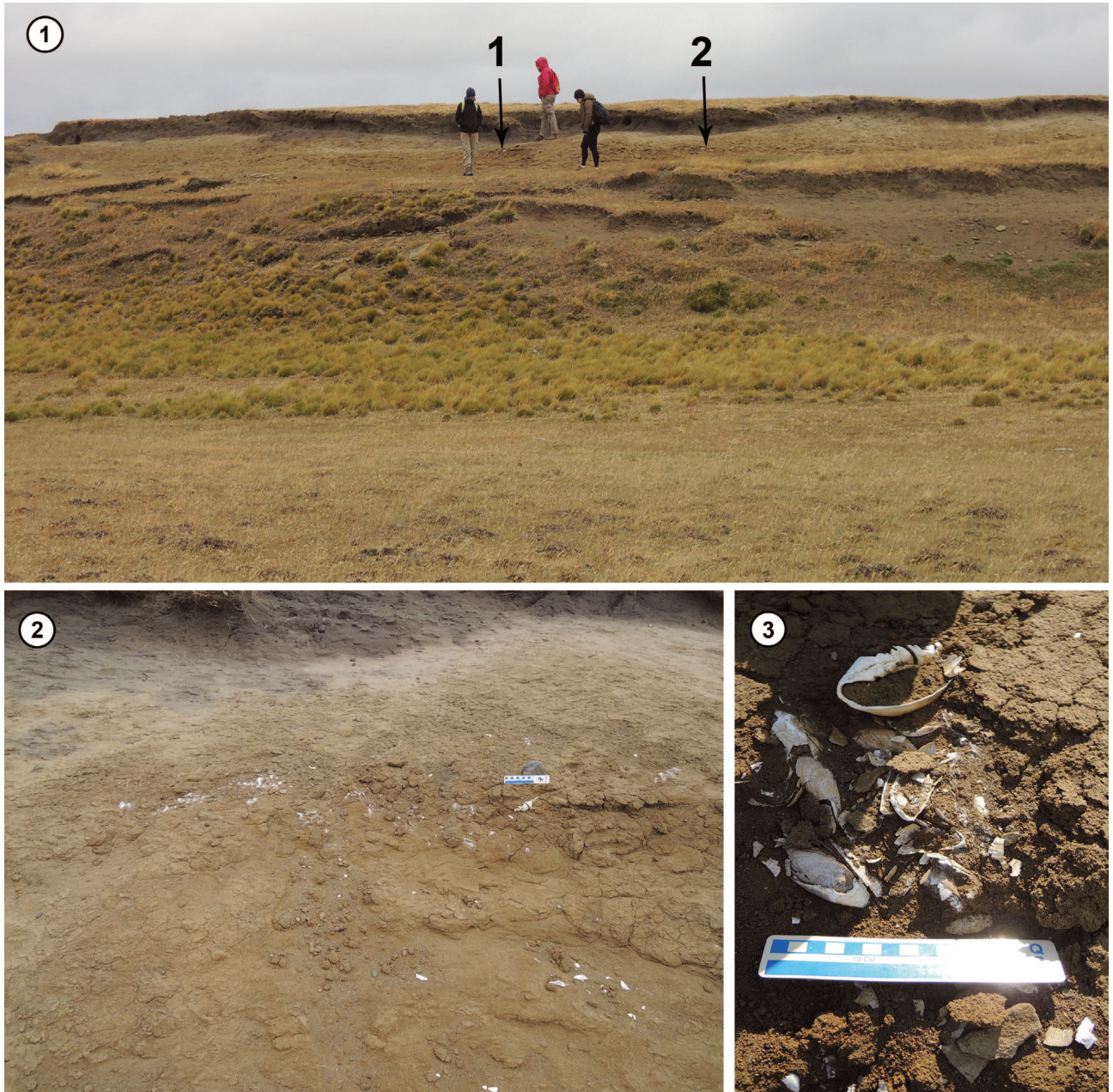


Figure 3. Shell lens on the southern hillside of Cerro Bandurrias. 1, Location of the 2.1 and 0.84 m segments of the lens, indicated by 1 and 2, respectively; 2, General view of Cerro Bandurria shell lens; 3, detailed view of the shell lens. Scale bars= 10 cm.

interpretation of the stratigraphy was also possible due to further regional field observations and prior research on analogous pedosedimentary sequences (Ozán, 2015; Borrazzo *et al.*, 2025). Stratigraphic and sedimentological properties were assessed through texture analysis by feel (USDA triangle, plus visual gravel estimation), color determination (Munsell Color, 1992), and structures observations (type and degree; Birkeland, 1999; Soil Survey Staff, 1999). Analytical data comprised pH measurements (1:2.5 solution in Milli-Q distilled water, Arcano PHS-3E Instrument) and electrical conductivity (EC, mS/cm; Hanna Instrument), with the latter serving as an indirect indicator of seawater influence on sediments (Grayver, 2021). Additionally, bulk magnetic susceptibility (m^3/kg ; mass-normalized) was measured at 200 Hz and 1000 A/m using a Kappabridge instrument, to detect sediment combustion signals (Ozán *et al.*, 2020 and references therein). These analyses were conducted on the surveyed stratigraphic section and on one off-site sample. While stratigraphic analysis focused on identifying depositional and post-depositional processes, analytical methods aimed to distinguish between anthropogenic and natural influences.

A vertebra of Osteichthyes was radiocarbon dated at DirectAMS Radiocarbon Dating Services, USA (sample code: D-AMS 048513). Radiocarbon dates were calibrated with Oxcal 4.4 (Bronk Ramsey, 2021) and by using the Marine20 curve (Heaton *et al.*, 2020), at 2σ (95.4%). The local ΔR correction applied for marine resources was 265 ± 45 (Cordero *et al.*, 2003).

RESULTS

Analyses of biogenic content

Bioclasts in the sample include shells and bones. Table 1 summarizes the weight of the different components. Bioclasts represent ~13% of the weight of the sample recovered.

Description of exoskeletal concentration. According to Kidwell *et al.* (1986) and Kidwell & Holland (1991), the Cerro Bandurrias shell lens is a simple exoskeletal concentration. Its taxonomic composition is polytypic (Mollusca and Vertebrata) and paucispecific (*i.e.*, with a few represented, strongly dominated by one species; see below). Cerro Bandurrias lens is also an allochthonous assemblage (*i.e.*,

TABLE 1 – Sample composition and weight.

		Weight (g)	%
Matrix	Sediments	3331.20	87.05
	Mollusca	467.79	12.22
Bioclasts	Vertebrata	27.71	0.72
	Total	3826.70	100

composed of transported specimens out of their life habitats).

Regarding its biofabric, shells in the cross-section of the deposit exhibit an oblique orientation; in portions, clustering stacking—without preferential concave-up or concave-down—and nesting patterns are observed in the cross-section (Fig. 4.1–4). The accumulation varies from dense to loosely packed, and it ranges from bioclast to matrix supported. It is poorly sorted and, according to the geometry of the deposit, it can be classified as a thin lens.

Taxonomic composition. The bioclasts in the sample are represented principally by seashells—bivalves and gastropods—and a few fish bones (Fig. 5.1–4). Only 107 (1.52%) out of the 7035 fragments of mollusks were identified to genus and species level (Tab. 2).

Mytilus chilensis is the most represented species in the malacological assemblage. The minimum number of individuals (MNI) is 53 (according to the right valves count). One of the bivalves could only be determined at the Class level due to preservation issues of its outer features (Fig. 4.3). Gastropods are represented by the genus *Odontocymbiola* sp. (MNI = 4), some of which are fragmented shells that preserve their diagnostic features (Fig. 5.2). The scarce vertebrate specimens recovered ($n = 138$) were identified primarily as fish bones, including at least one *Genypterus blacodes* specimen (Tab. 2).

Chronology. A vertebra of Osteichthyes (Fig. 5.3) recovered from Cerro Bandurrias shell lens was radiocarbon dated in 6566 ± 35 ^{14}C years BP (D-AMS 048513; 6736–6348 cal. years BP; median: 6544 cal. years BP). This calibrated date is similar to the chronology of the Rio Chico 1 archaeological site (Santiago, 2013), located ~50 km to the southeast of Cerro Bandurrias.

Taphonomy. The material—mainly composed of Mollusca—shows low prevalence of destructive factors. The assemblage was dominated by whole specimens while contained in the sedimentary matrix. However, due to their fragility, all the shells broke when they were removed from the sediments at the lab, overestimating the non-natural fragmentation produced by the cleaning procedures (Fig. 6.1). The chemical alteration of shells is also manifested in their chalky and porous aspect as well as the reduction of their weight. Among the *Mytilus chilensis* specimens, fragments ranged from 0.7 to 4.6 cm. Only six *Mytilus chilensis* have more than 90% of the valve complete with the individual diagnostic element present which have an average length of 3.26 cm (min. 2.12; max. 4.6 cm). While this information is not representative of the sizes of this bivalve sample, it shows the presence of specimens of different sizes, with no clear trends in this species. The whole bivalve specimen not determined exhibits the largest size in the assemblage (6.19 cm). The *Odontocymbiola* sp. specimens were all fragmented and they measured between 5.6 and 7.2 cm. Similarly, more than 69.5% of the fragments of indeterminate mollusks exhibited 0.1 to 0.6 cm in length (fragmentation that has a methodological source—cleaning).

Among bivalves and gastropods exfoliation, cracks, abrasion (Fig. 6.2) and loss of periostracum are the taphonomic features with the highest prevalence, with the addition of root marks and chemical dissolution in the *Mytilus* specimens (Fig. 7.1). The same attributes with different frequencies are observed among indeterminate mollusks (Fig. 7.2). Among bioerosion traces, we only considered the presence of marks related to perforations and encrustations. Very low frequencies of these kinds of traces were recorded (e.g., perforation at the apex of a *Mytilus*), which would have occurred on the living specimen. A more in-depth evaluation and detailed quantification of bioerosion marks will be conducted in the future. On balance, the bioclasts show a low prevalence of destructive

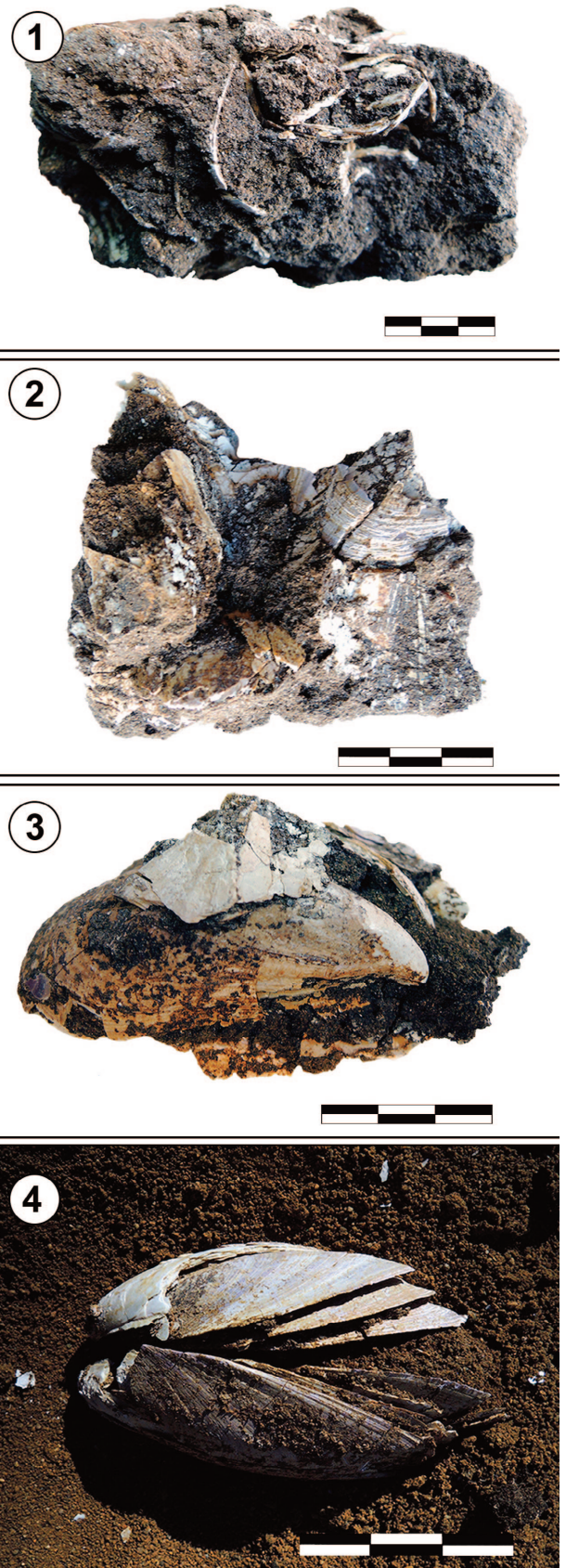


Figure 4. Examples of clustering patterns exhibited by shells in Cerro Bandurrias lens. 1–3, stacking (three different views); 4, nesting. Scale bar = 3 cm.

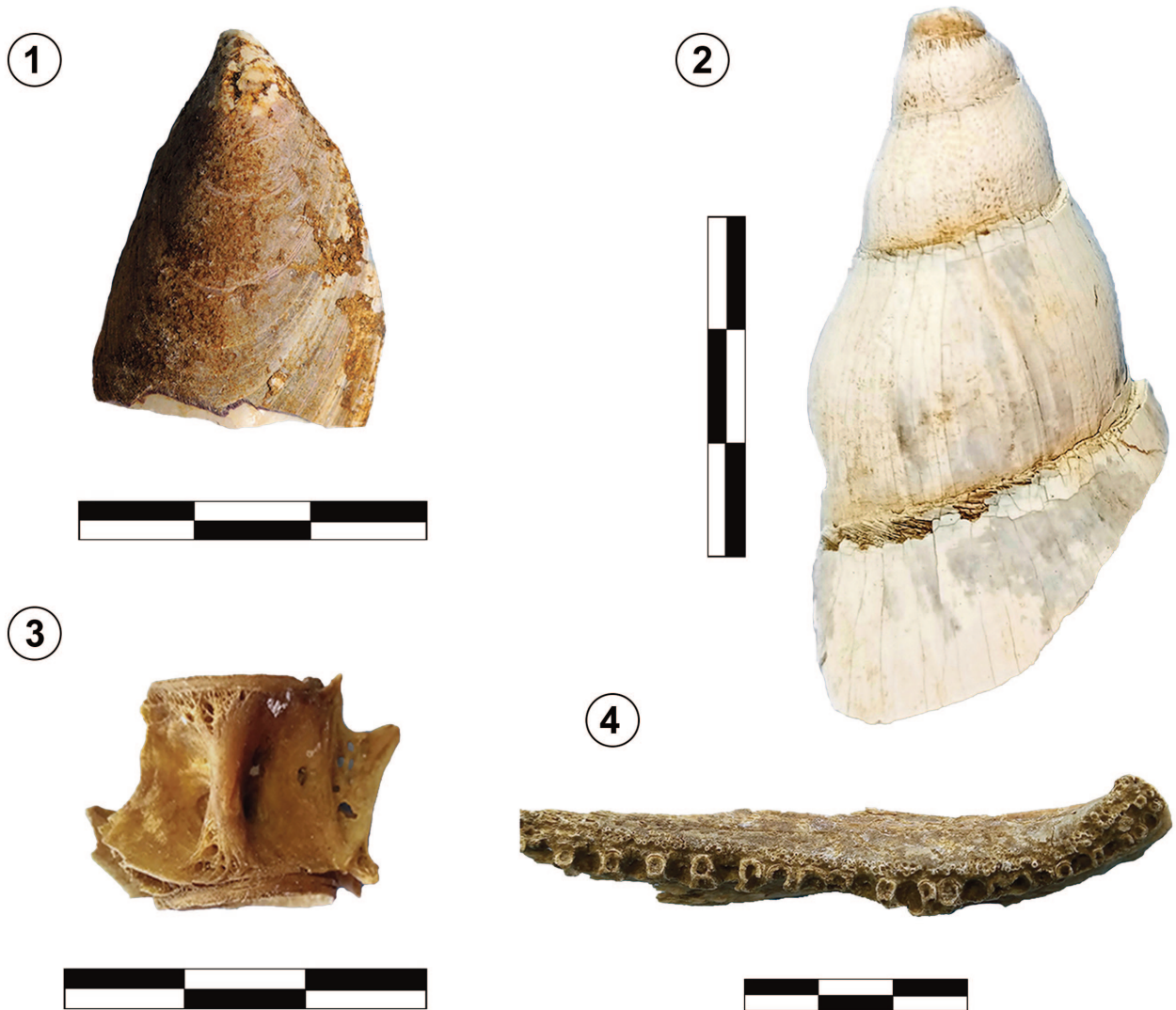


Figure 5. 1, *Mytilus chilensis*. 2, *Odontocymbiola* sp. 3, Radiocarbon dated Osteichthyes vertebra. 4, *Genypterus blacodes* mandible. Scale bar= 3 cm.

TABLE 2 – Taxonomic composition of the lens fauna.

	Taxa	n	%
Mollusca (n 7035)	<i>Mytilus chilensis</i>	102	1.45
	Bivalvia	1	0.01
	<i>Odontocymbiola</i> sp.	4	0.06
	Indeterminate	6928	98.48
Vertebrata (n 138)	Osteichthyes	88	63.77
	<i>Genypterus blacodes</i>	1	0.72
	Indeterminate	49	35.51
	Total	7173	100

factors, with fragmentation being the variable with the greatest weight.

Only two cases of root marks and one of cortical exfoliation were recorded among vertebrates. The latter corresponds to the lower jaw of *Genypterus blacodes*, which was found subaerially exposed at the recovery. The malacological and vertebrate fauna do not show unequivocal evidence of human manipulation (cut marks, formatting, polishing or decoration of the valves, and thermal alteration). The 5.88% of the bivalve remains show changes in their coloration (*e.g.*, brown and greyish tones; Figs. 5.1, 6.3).

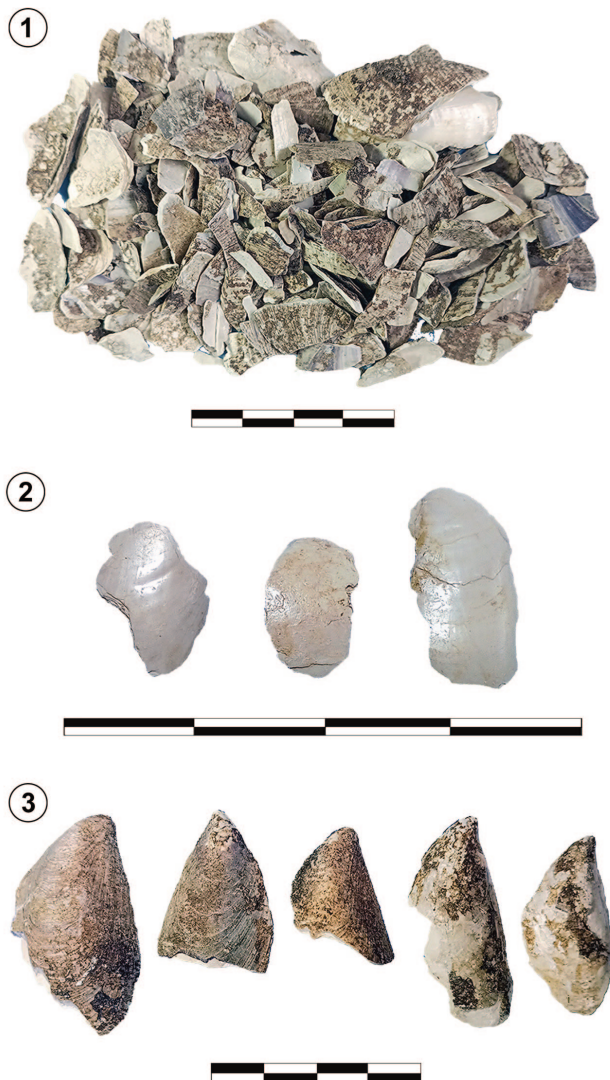


Figure 6. 1, Fragmented material of Mollusca. 2, Bioclasts with erosion. 3, Bivalves showing color change. Scale bar= 4 cm.

Stratigraphy and sedimentary characterization

In general, the studied archaeological section presents brownish sandy sediments, with different proportions of pelites (*i.e.*, silt and clay) and gravels, comprising poorly to moderate sorting matrices. The pH is neutral to slightly alkaline (7.1–7.7), and the electrical conductivity (EC) shows minimum variations (0.1–0.3 mS/cm). As expected, the pH (8.1) and EC (0.6 mS/cm) from the shell lens sample yielded higher values (Tab. 3). Values of magnetic susceptibility below and above the shell lens and in one off-site sample did not show differences.

From bottom to top, the section begins with the consolidated sandstone of the Carmen Sylva Formation and its regolith, inferred at about 170–160 cm depth since the entire section was not visible in a single exposition, rather in several scarp steps (Figs. 3.1, 8). Above (~160–155 cm depth), in clear contact, a light olive brown (2.5Y 5/4) thin loamy sand level with a weak angular structure is registered (L1 in Fig. 8). Examination of this level with magnification shows the presence of white saccharoidal coatings, filling voids, as cement, which do not instantaneously react with

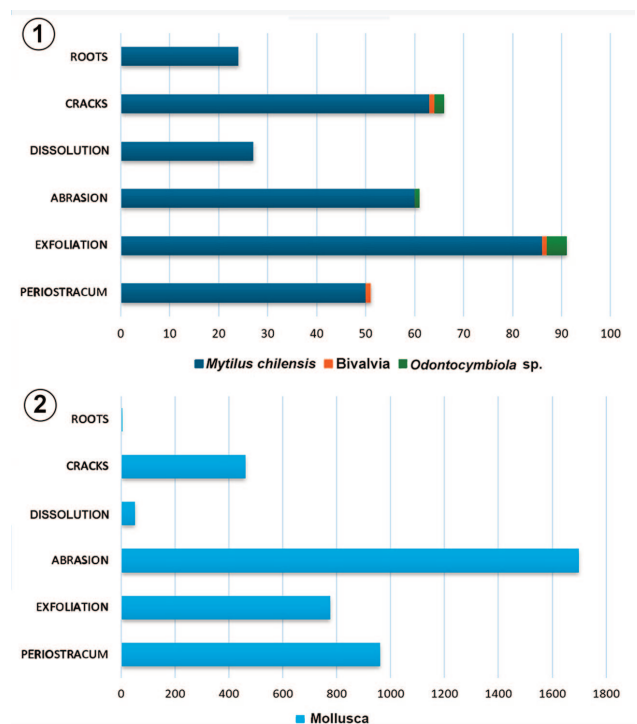


Figure 7. Predominant non-anthropogenic taphonomic variables. 1, Bivalvia and Gastropoda; 2, Mollusca indeterminate fragments.

TABLE 3 – Analytical data related to the stratigraphy of the studied section. Soil related variables following Soil Survey Staff (1999).

Descriptive stratigraphy	Sample depth (cm)	Texture	Color (Munsell color chart)	Structure	pH	Electrical Conductivity (mS/cm)	Magnetic Susceptibility ($\times 10^{-6} \text{ m}^3/\text{kg}$)	Comment
L1 (~160–155)	X ₁ (~160)	Loamy sand scarce subrounded gravels	Light olive brown (2.5Y 5/4)	Weak angular	7.7	0.25	2.97	Clear contact with lower level. Coatings in voids and grains
L2 (150–70)	X ₂ (~100). Next to the shell lens	Loamy sand with frequent subrounded gravels	Dark yellowish brown (10YR 4/4)	Strong angular	7.7	0.14	3.41	Gradual contact with lower level. REDOX features. Cementation
	X ₃ (~100). In the shell lens		White speckled in dark yellowish brown (10YR 4/4 matrix)	Massive	8.1	0.39	2.40	
	X ₄ (~100). In the shell lens		White speckled in dark yellowish brown (10YR 4/4 matrix)	Massive	8.0	0.32	2.19	
	X ₅ (~100). Ca. 10 m away from the shell lens		Dark yellowish brown (10YR 4/4)	Strong angular	7.8	0.16	3.03	
L3 (70/60–30)	n/s	Loamy sand occasional subrounded gravels	Brown (10YR 5/3)	Single grain	–	–	–	Clear contact with lower level
L4b (~30–20)	X ₆ (~25)	Loamy sand occasional subrounded gravels	Very dark greyish brown (10YR 3/2)	Weak sub-rounded/crumby	7.2	0.22	3.39	Gradual contact with lower level. High bioactivity
L4a (~20–0)	X ₇ (~10)	Sandy loam scarce subrounded gravels		Granular	7.1	0.26	1.80	Welded with lower level. High bioactivity (abundant roots)
Off-site	X (sup.)	Loamy sand scarce subrounded gravels	Brown (10YR 5/3)	Single grain	7.0	0.16	2.41	Sample was taken at the foot of a nearby outcrop (Cerro del Medio)

Abbreviations: L, level (depth in cm); X, bulk sample (see Fig. 8).

HCl (Fig. 8). It is likely that this illuviated cement comprised Si-bearing precipitations, coming from the sandstone weathering, as it was recorded at other archaeological contexts of northern Tierra del Fuego (Ozán, 2015). Dark and reddish coatings (iron/manganese oxides) are also observed in grains and matrix. In general, all these coatings are conspicuous features produced by illuviation from upper levels, likely related to the shell lens dissolution and mineral weathering. Poorly drainage conditions may favor manganese oxide precipitations.

From approximately 150 to 70 cm depth, a loamy sand level, with frequent subrounded gravels and a strong angular structure is observed in gradual contact with L1. This level (L2 in Fig. 8) depicts dark yellowish-brown hues (10YR 4/4), likely resulting from postdepositional processes related to REDOX conditions (*i.e.*, color) and illuviation (*i.e.*, structure). The occurrence of wet-dry cycles on this level is also observed through dissolution-precipitation features, expressed as cementations. This level contains the thin shell lens, placed around 100 cm below the surface.

Above (70/60–30 cm depth), in clear contact, it is registered a brown (10YR 5/3) single grain loamy sand level (L3 in Fig. 8). On the top of the sequence, and in gradual contact with L3, it is observed a very dark greyish brown (10YR 3/2) level, with a subrounded to crumbly weak structure only detected at the bottom (L4b in Fig. 8). Textures are also slightly coarser upwards (L4a in Fig. 8). These levels are clearly related to intense biological activity.

Given the presence of conspicuous edaphological characteristics such as color and structure, this sequence can be undoubtedly interpreted as a soil profile.

DISCUSSION

Depositional and postdepositional evolution

According to the regional geological and chronological

information already presented, the Cerro Bandurrias might have been a coastal landform by the time the shells accumulated at the locus (Isla *et al.*, 1991; Vilas *et al.*, 1999). Available data from the stratigraphic section studied here and the information from the sedimentary deposits on other neighbor sandstone outcrops (Favier Dubois, 1998; Ozán, 2015; Borrazzo *et al.*, 2025) allow to understand the sequence of the depositional and postdepositional processes that took place at the Cerro Bandurrias archaeological locality (Fig. 9). Textural and structural data (Tab. 3) suggest that the parent material upon which soil forming factors occurred were deposited by aeolian processes. The rather poor sorting of these sands may be explained by the frequent and high average wind speed in the region, which reaches over 150 km/h, particularly in the

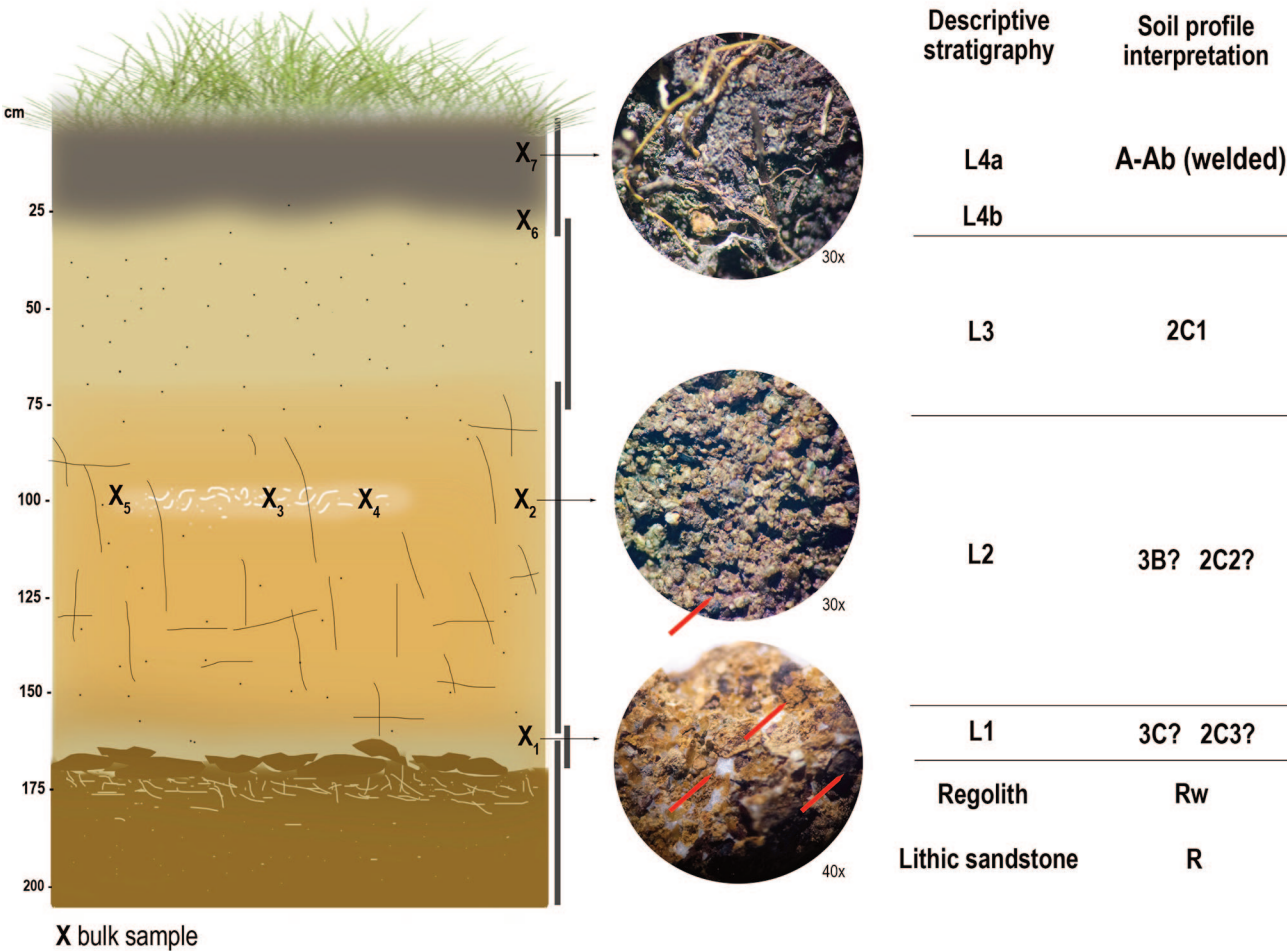


Figure 8. Schematic stratigraphy of Cerro Bandurrias shell lens. Nomenclature refers to a descriptive (left column) versus interpretative (right column) stratigraphic analysis. Red arrows point to the record of (white, red, and black) coatings under the stereomicroscope. Additional analytic data is in Table 3.

summer season (e.g., Vilas *et al.*, 1999; Borrazzo, 2016). This fact poses a pitfall in traditional aeolian literature, where wind deposits are usually characterized by good sorting (Gillies *et al.*, 2012; Wang *et al.*, 2022). In addition, the visual examination of the sand under magnification may indicate that the source of such material is the weathered consolidated sandstone, along with a finer fraction transported by suspension, may be coming from the surrounding lakes (Figs. 1–2).

The shell lens was likely deposited and buried during an aeolian accretion phase, in the context of the Middle Holocene marine transgression (e.g., Bujalesky, 1998). Rapid sedimentological rate might have favored the preservation of the lens and its content (*i.e.*, predominance of whole shells, presence of small-size fish bones) in line with relatively arid conditions (Laprida *et al.*, 2021). Afterwards, two possible scenarios can be inferred from available data (Fig. 9): one related to (A) pedogenesis and another associated to (B) the existence of a cyclical—maybe seasonal—water accumulation. Scenario A is supported by the presence of root marks on some bivalves. In this case, the reddish and structured level could be interpreted as a B soil horizon of a “decapitated” paleosol profile. Such well-developed soil formation, which includes a B horizon, was reported in the Arturo perched dune, before *ca.* 3000 cal.

years BP (Coronato *et al.*, 2020; Musotto *et al.*, 2022), in the context of some wet pulses (Coronato *et al.*, 2020, 2022; Laprida *et al.*, 2021).

Scenario B is explained by the periodic permanence of water, likely related to seasonal melting cycles (Fig. 10). This situation might have caused strong REDOX conditions, evidenced in reddish hues and illuviation features, such as the coatings described (Fig. 8). The above-mentioned wet phases could also apply for this B scenario. Beyond which scenario matters in the depositional evolution, it is worth mentioning that the reddish and angular structure of this level correspond to postdepositional processes that took place after the shell lens was deposited, hence they are not contemporaneous. Redox conditions, however, have affected the shell preservation. Although color alteration may result from the exposition of shells to fire (e.g., Villagrán, 2014; Hammond, 2015), its occurrence in Cerro Bandurrias lens is more probably a diagenetic feature related to water accumulation.

Wind sedimentation (*i.e.*, accretion) continued until a well-developed soil took place. This pedogenesis could be attributed to any of those reported regionally for the Late Holocene (e.g., Favier Dubois, 2003; Ozán *et al.*, 2015; Coronato *et al.*, 2020, 2022). An active morphogenesis then buried that soil, and another—yet weak—pedogenesis

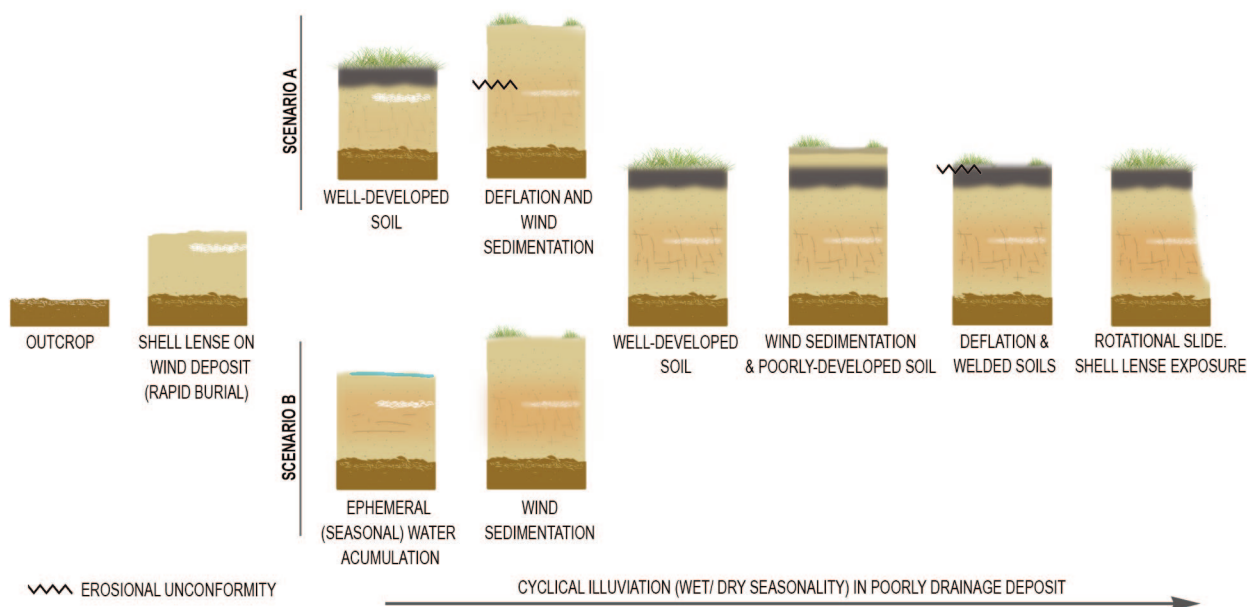


Figure 9. Schematic evolution of the shell lens stratigraphy.



Figure 10. The Cerro Bandurrias locality under a snow cover (June 2024). Also note the presence of sheep (Photo: David Cantero).

occurred (present conditions). In the analyzed section, this last wind deposit was deflated, so the present top soil reset by taking the paleo A (buried) horizon as parent material, resulting in “welded A horizons”. In other nearby exposed section, the present soil profile has kept its original parent material.

Shell lens genesis

Several factors preclude ruling out natural or cultural processes as the primary mechanisms for shell accumulation. First, based on the San Sebastian Bay’s coastal evolution and the chronology of the fish remains in the lens, the ocean might have been near the locus when the skeletal accumulation occurred. Second, the shell lens lacks univocal anthropic traits (*e.g.*, lithic artifacts, cut marks on bones, polished bones, decorated valves, burnt shells, charcoal). Thus, the Cerro Bandurrias shell lens becomes a genetically challenging deposit. In this regard, three hypotheses concerning the shell accumulation at Cerro

Bandurrias are discussed, drawing on different agents and processes. We derive material expectations for each depositional process and then compare and contrast them with the fossil record.

Hypothesis 1: shell lens as a geogenic deposit. This explanation proposes that the natural coastal processes were the primary depositional mechanisms for the shell accumulation. Thus, the shell lens would represent coastal sedimentary facies. As mentioned, Cerro Bandurrias was surrounded by the sea when the shell lens formed (~6500 cal. years BP). All the mollusk species represented in the shell lens are living on the San Sebastian Bay and the Atlantic coast nowadays (Gigli & Loekemeyer, 2011; Santiago *et al.*, 2014), and their shells are usually found on the beach. For *Genypterus blacodes* biological data indicates that this species is living in the region (*e.g.*, Cordo, 2004; Gigli & Loekemeyer, 2011). Geological studies established that the Middle Holocene sea level in San Sebastian Bay and the area of Bueno and Chico rivers were located between

1.5 and 2.7 m above the current storm berm (Montes, 2015; Coronato *et al.*, 2022). Indeed, a value of +1.57 masl was indicated for the Middle Holocene maximum transgressive coast in San Sebastian Bay (Bujalesky, 2007; Montes *et al.*, 2018, 2020). The highest sea level position during the Middle Holocene was not high enough to deposit the shells on the hilltop of Cerro Bandurrias. The shell lens is located at 10 masl, so the locus was out of reach of the flood during the marine transgression. Therefore, the Cerro Bandurrias shell lens cannot be explained as a beach deposit.

The record of Holocene active tectonics is abundant in IGTFD (*e.g.*, Winslow & Prieto, 1991; Bujalesky, 2007). San Sebastian Bay is part of the Inutil-San Sebastian depression, which is bounded by ENE-WSW-striking normal faults (Diraison *et al.*, 1997). This structural configuration is consistent with the regional ENE-WSW convergence of the South American Plate and with neotectonic deformation documented along major regional faults, such as the sinistral strike-slip Magallanes-Fagnano Fault System (*e.g.*, Diraison *et al.*, 1997; Bran *et al.*, 2023). Given that this fault-bounded block has been subsiding as part of a structural depression over the past million years, it is unlikely that the archaeological shell lens under study was located at a lower elevation in the past, thus reducing the probability of past marine floodings. Indeed, the regional study conducted by Montes (2015) at the Chico River (~50 km to the south of Cerro Bandurrias) highlighted the tectonic stability of the area and reported a local relative elevation rate of 0.352 mm/year. These data indicate that the locus of the shell lens at Cerro Bandurrias remained above the sea level during the Holocene.

There are, however, coastal sedimentary facies that do not require flooding for their formation. Cliff-top storm deposits (CTSDs; Smith *et al.*, 2014) are shelly and sandy deposits comprising a fringe adjacent to the marine cliff top. Its deposition is patchy but only found within 10 m from the cliff edge. According to Smith *et al.* (2014), CTSDs are emplaced as air thrown from waves and wind-borne plumes produced by the bores of broken waves striking the base of the cliffs. Occasional rounded pebbles (0.5 to 1 cm diameter) are present in the CTSDs. Other characteristics of these deposits include: (A) dominance of fragmented shells (exhibiting variable weathering and age), and (B) shell

fragment's frequency and size increase towards the cliff edge. As we mentioned, shells at the lens were mostly complete while contained in the sedimentary matrix at Cerro Bandurrias. Furthermore, the homogeneous depth and the limited lateral extension of Cerro Bandurrias shell lens suggest that the marine remains resulted from a single or few events occurring during a short period. In addition, although postdepositional processes might have affected the parameter, electrical conductivity values—which are indicative of the presence of total salts—are lower at Cerro Bandurrias sediments (0.14–0.39 mS/cm) than actualistic reference values of marine sediments, like tidal marshes, inter-tidal or backshore deposits (4 and 15 mS/cm) or also berms (1.7 mS/cm) (Ozán, personal observations). In sum, the characteristics of the biogenic content (*i.e.*, whole specimens of few species), the lateral extension, and the geomorphological information do not support the matrix of Cerro Bandurrias lens is of marine origin nor the sedimentary features that characterize the influence of the coastal processes.

Hypothesis 2: ornithogenesis. San Sebastian Bay is a prime habitat for many species of birds, including several migratory shorebirds that feed in its large intertidal mudflats (López Gappa & Cruz Sueiro, 2007). The second hypothesis examined here proposes that seabirds were the primary agents of deposition for the Cerro Bandurrias shell lens, representing the accumulation of food remains left by birds such as seagulls (*Larus* sp.), cormorants (*Phalacrocorax* sp.), oystercatchers (*Haematopus* sp.) and other species that include mollusks and fish in their diets (*e.g.*, Tobar *et al.*, 2019). Naturalistic observations available on the predation patterns of these sea birds report the swallowing of whole fish, the scavenging *in situ* of large fishes stranded on the coast, and the shellfish foraging on the littoral bed and the shoal (*restinga*) (*e.g.*, Demongin, 2008). Oystercatchers may crack the shells of bivalves with their beak to eat the soft tissue at the mussel bank (*e.g.*, Bernat, 2024). Other seabirds that cannot break the shells with their beaks may carry the shellfish up in the air and then drop them from a height onto a hard surface (Ingolfsson & Estrella, 1978). Once the shells crack, the bird eats the flesh. The content of seabird egagropiles may include fish and small mammal bones and mollusk and crab shell fragments. These pellets

are less cohesive than non-marine bird egagropiles and tend to disaggregate when they are primarily made up of animal remains (Bang & Dahlstrom, 1975). Areas frequented by sea birds may accumulate shells and bone remains on the surface, exhibiting scattered distributional patterns. If a flat surface is available, the food remains extend in a low-density, homogeneous scatter showing no preferential distribution or concentrations. Fragmented shells are more abundant than whole shells in those scatters.

The bivalve and gastropod shells of Cerro Bandurrias

lens displayed a high degree of completeness while in the sedimentary matrix. As we mentioned, the fragmentation of the malacological specimens reported is related to the fragility of the diagenetically altered calcareous valves and, principally, to the subsequent process of cleaning and conditioning in the laboratory. Also, the limited spatial extension of the shell accumulation as well as its biofabric do not favor the ornithogenesis hypothesis. Therefore, the formation of the discrete lens mainly composed of whole shells of few species in Cerro Bandurrias hilltop is unlikely explained as seabird food remains.



Figure 11. "Common miner" (*Geositta curricularia*) at the Cerro Bandurrias shell lens (Photos: Catalina Balirán). 1, Entrance of the tunnel excavated by the common miner to build its nest; 2, "Common miner" standing by the entrance of its nest; 3, "Common miner" entering the tunnel. Scale bar= 10 cm.

However, it is worth mentioning that we recently confirmed the impact of small birds on Cerro Bandurrias shell lens. During fieldwork in 2024, we observed that a common miner (*Geositta curricularia*) had built its nest within sector B of the exposed shell lens. The common miner excavated a horizontal tunnel in the shell-rich layer (Fig. 11.1–3). The taphonomic effects of this process include the removal of bioclast and sediments from the stratigraphic unit and the addition of exotic elements to prepare the nest, such as vegetal tissue, food remains, feathers as well as the incidental deposition of bones due to a bird's death. Therefore, this nesting behavior causes the partial destruction of the fossil deposit, alter its biological content, and may promote modifications in the stratigraphy as the tunnels collapse.

Hypothesis 3: archaeological shell midden. The third explanation explored here raises the possibility that the Cerro Bandurrias shell lens is an anthropogenic deposit. As mentioned, shell middens can vary in size, ranging from large mounds to thin shell lenses. When it is present, thermal alteration is a diacritic of the anthropogenic origin of shell-rich deposits (e.g., Waselkov, 1987; Claassen, 1998; Beovide *et al.*, 2015; Villagrán *et al.*, 2021). Shell middens are typically found close to coastlines, as they are produced by humans foraging in littoral beds and banks. Fuegian and global ethnographic accounts indicate that shellfish gathering among hunter gatherers is an activity primarily conducted by women (e.g., Meehan, 1975; Gusinde, 1991; Gallardo, 1998). Both the mode of deposition of shells in the archaeological record and the transformations observed after consumption sustain the relevance of Meehan's (1975) observations for IGTFD. The mollusks are collected from the shell bed by hand or using a slate fragment, a pointed or spatula-like wooden stick to help remove the shellfish from the rocks; they usually deposited the mollusks in a basket or a dilly bag (e.g., Meehan, 1975; Gusinde, 1991; Gallardo, 1998). Historical records refer to the *Selk'nam* people inhabiting the northeastern coast of IGTFD collected mollusks when the tide had receded from the beds so that they were exposed (e.g., Chapman, 1986; Gusinde, 1991). In her ethnographic study on northern Australian fisher-hunter-gatherers, Meehan (1975) notes that the shellfish was transported to the camp and

immediately cooked. Mollusks were roasted on the coals of a small fire, designed to be fast and hot, and usually only burned for a few minutes (Meehan, 1975, p. 137; Waselkov, 1987). The shells opened when exposed to heat (Waselkov, 1987). The flesh was easily removed and the juice left in the shells after cooking was consumed. Shells were discarded where they had been eaten, forming discrete piles in which pairs of valves attached by the gristle are abundant (e.g., Meehan, 1975). In sum, the activities involved in the manipulation of shellfish for human consumption include gathering from the shell bed, transport, cooking (required for opening bivalves), and discarding shells.

In southern Patagonia, archaeological shell-bearing deposits are recorded up to 80 km from the marine coast (Borrero & Barberena, 2006). These are small cultural shell accumulations that include or are spatially associated with artifacts (e.g., tools) and ecofacts (e.g., food remains) of other raw materials (bone, lithic, pottery, wood, charcoal, etc.) which are more abundant and diverse in large shell middens. The latter are coastal archaeological sites, except for Orejas de Burro which is located 17 km from the coast (L'Heureux, 2008). For the archaeological record on the Fuegian Atlantic coast, a 5 km radius from the coastline was proposed as threshold for regular marine resource consumption (Borrero, 1985).

As mentioned before, the inspection for anthropogenic attributes in the shell assemblage did not provide unequivocal evidence of human exploitation of the mollusk and vertebrate remains. The change in the coloration of bivalves' calcareous surfaces is probably a natural consequence of the contact of the valves with the matrix affected by the cycles of illuviation (see above), and it may not necessarily be a consequence of an intentional thermal alteration aimed at preparation or cooking food. Therefore, assessing the anthropic or non-anthropic character of the Cerro Bandurrias shell lens requires moving the focus to attributes related to the regional context, the depositional history of the lens, and the taxonomic composition of its biologic assemblage.

Among the general attributes exhibited by the remains of mollusks associated with human exploitation could be considered (A) lower taxonomic diversity than the local naturally available (e.g., while modern Fuegian Atlantic

beach assemblages include 13 to 9 taxa, archaeological assemblages exhibit only 6 to 3 mollusk species; Santiago *et al.*, 2014); (B) size sorting due to the selection of larger specimens to enhance edible tissue; and (C) low frequency of bioerosion because the live specimens are gathered for consumption (Henderson *et al.*, 2002; Beovide *et al.*, 2015). Shells in anthropogenic deposits may exhibit low fragmentation, since harvested bivalves are transported and deposited out of the taphonomic active zone and opened up on exposure to heat (*e.g.*, Meehan, 1975). Therefore, the completeness of shells may indicate a rapid burial and that they did not remain dead in their natural context. In addition, among hunter-gatherers without navigation technology like the northern Fuegian groups (Borrero, 2001), fish have to be accessible from the coast. Torres (2009) summarized the references available for fishing practices in Fuegian ethnographic accounts. These historical sources informed that northern Fuegians gathered fish and shellfish on rocky shores, also from tide pools, and under stones during the low tide where the intertidal zone extends for more than 2 km or where marine fauna strands (Chapman, 1986; Gusinde, 1991; Coiazzi, 1997; Gallardo, 1998).

Bioclasts in Cerro Bandurrias shell lens are dominated by *Mytilus chilensis*. Gigli and Loekemeyer (2011) stated that *Mytilus chilensis* and *Brachidontes purpuratus* are the more abundant bivalves in the San Sebastian Bay, living fixed by the byssus in the intertidal and sublittoral zones. Although mollusks of Cerro Bandurrias lens are highly fragmented, the shells were complete while they remained in the matrix. The low diversity of species and the dominance of whole specimens are attributes that favor the anthropogenic hypothesis. Due to fragmentation, size sorting cannot be accurately assessed in the Cerro Bandurrias assemblage.

Los Chorrillos, 21 km southeast from Cerro Bandurrias, is the only archaeological locality exhibiting abundant anthropogenic shell-rich deposits in San Sebastian Bay. It is situated on the southern coast of the bay and adjacent to the open Atlantic coast (Fig. 1.2). Human occupation at Los Chorrillos took place on a dune field since *ca.* 1000 years BP (Borrero *et al.*, 2008). Unlike large shell middens from other archaeological contexts, such as Punta María (Borrero, 1985) or the Beagle Channel (Orquera & Piana, 2000, 2001),

even in the densely reoccupied archaeological *loci* of Los Chorrillos, shell accumulations are thin (10 cm) horizontal bioclast-supported lenses or matrix-supported shell-rich deposits (Borrazzo & Borrero, 2016). *Mytilus chilensis* is the primary mollusk represented, exhibiting sizes of 5–6 cm, followed by a minor contribution of *Aulacomya atra*, *Nacella* spp., and *Odontocymbiola* sp. (Horwitz, 1995). The presence of *Nacella* spp. in the archaeological record of Los Chorrillos is related to the *restinga* available at the locality that constitutes the only rocky bank on the coast of San Sebastian Bay. Horwitz (1995) suggested that the contribution of *Nacella* spp. increased in the archaeological assemblages located on the Atlantic coast dated after 1000 years BP. Santiago *et al.* (2014) highlighted a spatial trend in shellfish species represented in archaeological shell-rich deposits of the Fuegian Atlantic coast: the dominance of mytilids in assemblages located to the north of Chico River and limpets in the south, probably associated with the different types of substrates that prevail in these two littoral regions and the ecologic requirements of each species. The northern Atlantic coast exhibits alternating rocky bottoms and the presence of sandy and gravelly facies that favor the anchorage of mytilids such as *Mytilus* or *Aulacomya*, which are fixed to these bottoms through the byssus. South of Chico River, the coast presents a more abundant hard substratum adequate for the limpets. According to the chronology of the geomorphological evolution of the bay, the Cerro Bandurrias shell lens was deposited before the formation of the beach barrier lagoon system on which the dune field of Los Chorrillos is located (Vilas *et al.*, 1999). Therefore, human occupation at the latter archaeological locality was only possible at least several centuries later (after 5200 years BP).

A pink cusk eel was identified within the fish remains of Cerro Bandurrias shell lens. *Genypterus blacodes* adults tend to inhabit submarine canyons, at the edge of the continental shelf. In Patagonian waters, they move to shallower depths in spring and summer where they can get caught in little pools of water. The current maximum observed size in female specimens of this species is 140 cm in length and 14,200 g in weight (Cordo, 2004). Although *Genypterus blacodes* is available year-round, its systematic fishing occurs nowadays between January and April, when it is

more abundant (Instituto Nacional de Investigación y Desarrollo Pesquero, 2025). Torres (2009) referred to the ethnographic consumption of scaleless fish, such as *Genypterus blacodes* or *Austrolycus* sp., collected at the coast by the *Selk'nam* during the months of the summer and the beginning of autumn. Also, Campan and Piacentino (2004) mentioned that pink cuskeel gets closer to the coast during the spring and the summer (Lloris & Rucabado, 1991). Therefore, the presence of *Genypterus blacodes* in the Cerro Bandurrias shell lens would be an indicator of the seasonal human use of the coastal resources. *Genypterus blacodes* has been identified in the Late Holocene ichthyoarchaeological assemblages of the San Genaro 1 and 2 sites (Los Chorrillos locality) where the medium and large size specimens were the most represented (Campan & Piacentino, 2004; Fig. 1.2). Also, it has been recorded in Late Holocene archaeological sites located in the Inutil Bay (Marazzi 2 and 38; Torres, 2009) and on the Atlantic coast (Margen Sur archaeological site, Salemme *et al.*, 2019). More importantly, *Genypterus blacodes* is also represented in Middle Holocene archaeological assemblages of Rio Chico 1, on the Atlantic coast (Santiago, 2013; Fig. 1.1). Torres *et al.* (2024) point that cusk eel was consumed more between 7500 and 2800 cal. years BP in the Magellan Strait, in particular during the Initial Late Holocene (3400–2700 years BP), when it increases its contribution in the zooarchaeological assemblages. However, the authors report a marked decrease in the abundance of *Genypterus blacodes* in the archaeological record during the Recent Late Holocene (after 2700 years BP). In sum, adding the evidence from Cerro Bandurrias, *Genypterus blacodes* is a species represented in the Fuegian ichtioarchaeological record since the Middle Holocene, hence its generally low contribution suggests it remained an occasional resource for Fuegian hunter-gatherers.

Middle Holocene archaeological shell accumulations on the Atlantic slope are scarce. La Arcillosa locality (53 km to the south of Cerro Bandurrias) is integrated by three archaeological sites (LA 1, 2, and 3) that are located on the ravine of Chico River (Fig. 1.1). Like Cerro Bandurrias shell lens, they are deposited in aeolian sediments with poor drainage laying on the Carmen Sylva Formation. The LA 1 and 3 sites are thin shell lenses with *Lama guanicoe*

fragmented bones and very few lithic artifacts spatially associated (Salemme & Bujalesky, 2000; Salemme *et al.*, 2014). The LA 2 site is a shell lens with a primary human inhumation dated 6175–5744 cal. years BP (Santiago, 2013). The Rio Chico 1 site comprises an 8 m long, and 10 to 40 cm thick shell lens located in an eolian deposit (Fig. 1.1). *Mytilus chilensis* is the most represented species in La Arcillosa and Rio Chico shell accumulations, exhibiting sizes over 4 cm. *Aulacomya atra*, *Nacella* spp., *Mulinia edulis*, *Odontocymbiola magellanica*, *Pareuthria plumbea* and cirripeds are also present (Santiago, 2013). Both La Arcillosa and Rio Chico were coastal locations by the Middle Holocene but, due to coastal accretion, like Cerro Bandurrias, they became inland spots during the Late Holocene.

The nesting pattern in the lens cross-section exhibited by bivalves in Cerro Bandurrias may inform about the postdepositional history of shells before their burial (*i.e.*, the accumulation of shells after the hunter-gatherer's manipulation). After their deposition on the hilltop and while exposed on the surface, shells were probably subjected to wind action, the most powerful geomorphic agent of the Fuegian steppe. Aeolian erosion in the area is known for winnowing artifacts weighing up to 13 g from surface lithic scatters when the wind blows at 80 km/h (Borrazzo, 2016). Therefore, it is possible to suggest that *Mytilus* shells were reordered and accumulated by airflow while remaining subaerially exposed (likely for a brief period) until their final burial. In addition, the presence of small bones suggests that fish remains were deposited and buried while they were still covered by soft tissues. The latter fact also suggests the lens may have had a short subaerial exposure before burial.

Therefore, the locus on the southern hilltop of Cerro Bandurrias presented here together with the previously reported thin shell lens on the northern slope (Favier Dubois & Borrero, 2005) record reiterated occasional consumption of seafood by Fuegian hunter-gatherers at the locality. Thus, the hilltop of Cerro Bandurrias preserves the ephemeral record (*sensu* Borrero, 2023) of marine fauna exploitation by the Middle Holocene. Further dating of shells from the locus studied here will adjust the temporal frame for the lens formation and it also will allow exploring the persistence of this subsistence practice.

CONCLUSIONS

The assessment of the spatial, pedolithological, taphonomic, and compositional characteristics of the Cerro Bandurrias hilltop stratigraphic sequence suggests that the shell lens constitutes an anthropogenic deposit. The geoarchaeological assessment of the *locus* indicates that although the thin lens was buried rather rapidly after its formation, subsequent water-related postdepositional processes, favored by poor drainage and probably more humid conditions, introduced significant changes in the sedimentary matrix affecting shell preservation.

Cerro Bandurrias shell lens represents a new Middle Holocene archaeological context in the Fuegian steppe and provides additional evidence of human-sea relationship. It is the ephemeral record of a minor marine component in the human diet by Middle Holocene times, a trend shared with the Atlantic coastal archaeological contexts of similar chronology. The study of Cerro Bandurrias shell lens allows us to access the material remains of a strategy described in historical and ethnographic accounts but scarcely recorded in the archaeological literature. The presence of *Gnyphterus blacodes* in the assemblage agrees with the regional archaeological background. By the Middle Holocene, fish may have been a complementary marine resource acquired by the casual encounter and gathering of isolated specimens (stranded or trapped) during shellfish harvesting tasks.

The case of the shell lenses of Cerro Bandurrias also emphasizes the critical role of the archaeological interception (*i.e.*, the moment of the archaeological discovery) for this fragile archaeological record in the Fuegian steppe. Once exhumed, the evidence of these ephemeral occupations is subjected to highly dynamic processes, and therefore, its survey is only possible for a short period before its destruction (*e.g.*, northern shell lens in Cerro Bandurrias hilltop, Favier Dubois & Borrero, 2005; RCH6, La Arcillosa 1 and 3, Salemme & Santiago, 2017; Santiago, personal communication). Finally, the case of Cerro Bandurrias shell lens highlights that the conspicuous character of shells improves the visibility—and thus the detectability—of the archaeological record produced by short-term, non-redundant occupations of hunter-gatherers.

ACKNOWLEDGMENTS

We are grateful to the personnel and owners of the Fuegian establishments Estancia San Martín, Estancia Cullen, and Estancia Sara for their hospitality and support during fieldwork. We would like to thank A.F. Zangrando for the taxonomic identification of fish bones. We especially thank Alejandra Rojas and Fernando Santiago for their comments, contributions and criticisms that improved the final version of this paper. We thank the members of our research team, Catalina Balirán, Ornella Pizzi and Jesica Manini, who participated in fieldwork at Cerro Bandurrias. Finally, we wish to thank to PE-APA editorial, production and graphic teams for their advice and guidance to adjust the manuscript for its publication. This research was funded by Fondo para la Investigación Científica y Tecnológica de la Agencia Nacional de Promoción de la Investigación, el Desarrollo Tecnológico y la Innovación (FONCYT, Agencia I+D+i, grant PICT2018-02807) and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET).

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doi: 10.5710/PEAPA.15.07.2025.545

Recibido: 18 de abril de 2025

Aceptado: 15 de julio de 2025

Publicado: 20 de octubre de 2025



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TAPHONOMY OF DEATH ASSEMBLAGES OF THE FRESHWATER BIVALVE *CORBICULA FLUMINEA* (MÜLLER, 1774) (VENEROIDEA) AFTER THREE AND FOUR DECADES IN THE UPPER RÍO DE LA PLATA, URUGUAY

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Abstract. The invasive bivalve *Corbicula fluminea* has been known in the Río de la Plata for approximately 40 years. This decadal time-lapse fill a gap in taphonomic studies. Our study is the second to investigate taphonomic modifications on valves of this species in Uruguay, expanding the temporal resolution of the first. We divided the valve into four sectors and recorded fragmentation, periostracum loss, and corrosion, categorizing these attributes into three severity levels. We also observed no attempts at bioerosion and bioencrustation. The central sector is the most frequent among all samples, and the posterior one is the least frequent. The differences in damage were tested using the X^2 test, the Bonferroni correction, and an average taphonomic score. We evaluated the extent of taphonomic damage over time by comparing the average taphonomic score using Kendall's *tau*. The tests revealed several statistically significant differences. The umbonal and posterior sectors are differently represented, with the 2008 sample being different in both cases. The central and anterior sectors do not exhibit differences. Fragmentation exhibits differences in all sectors except the anterior over the years; category 0 is the most represented in all years and sectors. Periostracum damage shows no statistically significant differences in sectors or years; category 2 is the most represented. Corrosion differs among the three samples, varying over the years in different sectors; category 2 is the most represented. In conclusion, there are statistically significant differences in the sectors represented and in fragmentation. However, no linear trend was observed over the years.

Key words. Actualistic Taphonomy. Death assemblage. *Corbicula fluminea*. Río de la Plata. Uruguay.

Resumen. TAFONOMÍA DE LOS ENSAMBLES DE VALVAS DEL BIVALVO INVASOR *CORBICULA FLUMINEA* (MÜLLER, 1774) (VENEROIDEA) LUEGO DE TRES Y CUATRO DÉCADAS DE SU REGISTRO EN EL ALTO RÍO DE LA PLATA, URUGUAY. *Corbicula fluminea* es un bivalvo invasor en el Río de la Plata desde hace aproximadamente 40 años, un lapso que no ha sido prácticamente estudiado desde la Tafonomía. Este estudio es el segundo sobre la especie, expandiendo la resolución temporal del primero. Dividimos las valvas en cuatro sectores, registrando la fragmentación, el daño del periostraco y la corrosión, clasificando la intensidad de estos atributos en tres categorías. El sector central fue el más representado siempre, y el posterior el menos frecuente. Para evaluar las diferencias en el daño tafonómico usamos el test de X^2 , el de Bonferroni y un índice de daño promedio. Para correlacionar este índice con el paso del tiempo utilizamos la *tau* de Kendall. Los sectores umbonal y posterior están diferentemente representados, siendo la muestra de 2008 la diferente en ambos casos. El sector central y el anterior no exhiben diferencias. La fragmentación es diferente en todos los sectores excepto en el anterior, y la categoría 0 la más representada siempre. El daño del periostraco es similar en todas las muestras y sectores, siendo la categoría 2 la más frecuente. La corrosión es diferente entre las muestras, variando el sector afectado; la categoría 2 es la más representada. No encontramos signos de bioerosión o bioincrustación. En conclusión, se encuentran solamente diferencias significativas en la frecuencia de los sectores representados y en la fragmentación. De todos modos, no existe una tendencia a lo largo de los años ni para estos casos ni para el daño global.

Palabras clave. Tafonomía Actualística. Asociación de muerte. *Corbicula fluminea*. Río de la Plata. Uruguay.

ONE OF THE PRIMARY issues about taphonomic processes is the time needed to produce recognizable signatures. In other words, how much time is required to reach a given taphonomic condition? Recently, the answers have come mainly from evaluating death assemblages and experimental taphonomy (Kidwell, 2002; Kowalewski &

Labarbera, 2004; Martínez *et al.*, 2020a).

Time averaging in death assemblages comprises, at best, hundreds of years (Kidwell & Bosence, 1991; Flessa, 1993; Flessa *et al.*, 1993; Meldahl *et al.*, 1997; Kosnik *et al.*, 2009; Martínez & Rojas, 2023; Ritter *et al.*, 2023), meanwhile experimental taphonomy (*i.e.*, artificial conditions) in

real-time implies a resolution of months or a few years (e.g., Flessa & Brown, 1983; Briggs, 1995; Chattopadhyay *et al.*, 2013). The Shelf and Slope Experimental Taphonomy Initiative —SSETI— field experiment (Powell *et al.*, 2002, 2008, 2010, 2011a, 2011b; Parsons-Hubbard *et al.*, 2011) began around two decades ago, trying to recreate realistic conditions. Still, it implies direct human intervention by introducing samples into the environment.

Molluscan shells are one of the most frequent protagonists in the study of taphonomic processes because of their abundance in present and past assemblages along with their high preservation potential (e.g., Parsons & Brett, 1991; Powell *et al.*, 1992; Best & Kidwell, 2000a, 2000b; Erthal & Ritter, 2017).

The use of a mollusk bioinvader with a well-documented arrival time in a given area enables us to observe natural taphonomic processes in action on a timescale that is typically not achievable. Martínez *et al.* (2020b), Antuña *et al.* (2021), and Gómez *et al.* (2023) are a series of published papers that evaluate the shells from a taphonomic point of view of the invasive gastropod *Rapana venosa* (Valenciennes, 1846) in Uruguay, concluding that taphonomic damage is reached very quickly. Through a process that lasts approximately 20 years, taphonomic conditions equivalent to those observed in millennial shells can be achieved.

Regarding freshwater environments, Kusnerik *et al.* (2020) compared the taphonomic damage in the invasive gastropod *Melanoides tuberculata* (Müller, 1774) with that of the native *Polygyra septemvolva* Say, 1818 in Florida (USA), finding rapid shell alteration. Meanwhile, Gómez *et al.* (2021) investigated the taphonomy of the invasive bivalve *Corbicula fluminea* (Müller, 1774) in Uruguay. The present paper continues that work, reevaluating the samples used therein and adding a new one collected several years earlier. *Corbicula fluminea* has been present in Uruguay for approximately forty years (see Ituarte, 1982; Veitenheimer-Mendes & Olazarri, 1983; Clavijo, 2021), providing a decadal resolution for the taphonomic processes involved. The goal of this paper is to determine whether the conclusions reached previously using the invasive estuarine gastropod *Rapana venosa* are valid when applied to an invasive freshwater bivalve.

MATERIALS AND METHODS

Sampling was carried out on a Río de la Plata beach known as Barrancas de San Pedro (34° 21' 1" S; 57° 54' 60" W) (Fig. 1). This area is part of the upper and intermediate Río de la Plata, being its coast part of the "Southwest littoral" landscape (Evia & Gudynas, 2000; López Laborde, 2003). This zone is characterized by coarse sand and gravel beaches limited by sedimentary cliffs. Waves and currents are usually of low energy. Nevertheless, wind-dominated tides are important, sometimes reaching the base of the cliffs.

We collected by hand all bioclasts of *C. fluminea* larger than 10 mm found in a rectangle limited by the low tide line up to about 5 m towards the cliffs, along about 30 m parallel to the water line, on three occasions (March 2008, April 2016, and May 2018), obtaining 223, 318, and 303 bioclasts, respectively. The specimens are housed in the Departamento de Paleontología, Facultad de Ciencias, Universidad de la República.

For the record of taphonomic features, valves were delimited in four sectors: umbonal, anterior, central, and posterior (Fig. 2.1). Fragmentation, the integrity of periostracum, and corrosion were registered and recorded on a three-state scale in each of the sectors: Fragmentation, 0: more than 80% of the section of the valve is present, 1: between 80% and 20% of the valve is present, and 2: less than 20% of the section of the valve is present. Periostracum, 0: periostracum is present in at least 80% of the surface, 1: periostracum is present in 80 to 20% of the surface, and 2: periostracum is present in less than 20% of the surface. Corrosion, 0: less than 20% of the external surface has signs of corrosion, 1: 80% to 20% has corrosion, 2: more than 80% of the external surface has signs of corrosion. To facilitate comparisons, this scale is identical to that used in our earlier works on invasive species (e.g., Gómez *et al.*, 2023). Bioerosion and bioencrustation were not recorded in any bioclast.

Additionally, we calculated an average taphonomic score for total taphonomic damage and for each sector, using an adaptation of the formula developed by Meldahl *et al.* (1997): $g1+2(g2)+3(g3)+4(g4)/n$. We used 0, 1, and 2 for our categories rather than the 1, 2, 3, and 4 chosen by Meldahl *et al.* (1997), but because of operational problems, we avoided



Figure 1. Geographic location of the sampled locality. Image from Landsat/Copernicus 2023; Google Earth, accessed November 2023. Scale bar= 50 km.

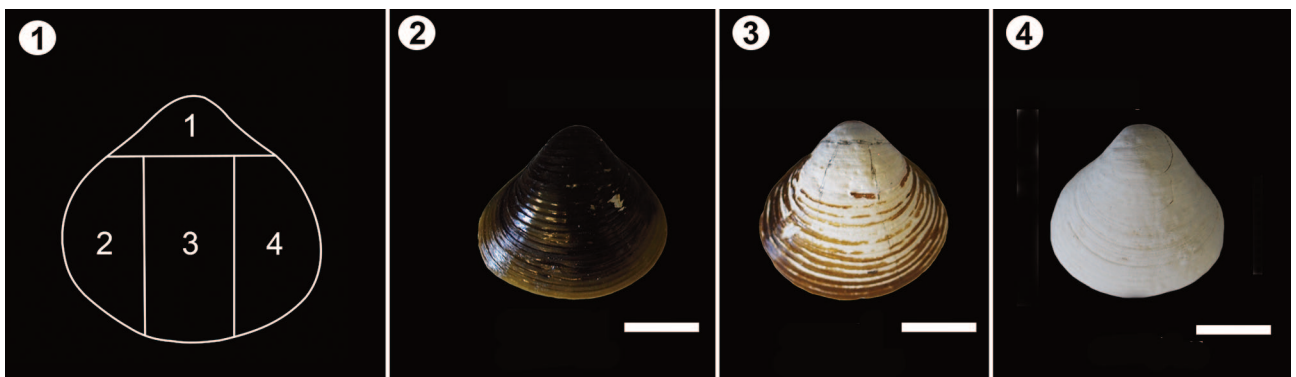


Figure 2. *Corbicula fluminea*. 1, Sectors of the valves: 1, umbonal; 2, anterior; 3, central; 4, posterior. 2, Shell illustrating fragmentation, periostracum, and corrosion category 0. 3, Shell illustrating periostracum and corrosion category 1. 4, Shell illustrating periostracum and corrosion category 2. Scale bar= 1 cm.

the 0 for the equation. Hence, the categories became 1, 2, and 3, and a new term (-1) was introduced to the equation, resulting $(c1+2(c2)+3(c3)/n)-1$. Here, $c1$ represents the shells included in our category 0, $c2$ those in category 1, and $c3$ those in category 2; n is the total number of shells, and the (-1), as said above, is introduced to compensate for the use of different numbers for the categories.

Data (Tab. 1) were summarized in histograms and compared using the *chi*-squared (X^2) test, with a $p < 0.05$ significance level. For pairwise comparisons, the post hoc Bonferroni correction was applied. To evaluate temporal tendencies, we used Kendall's *tau* correlation. The software used was PAST, version 5.2.2 (Hammer *et al.*, 2001).

TABLE 1 – Number of bioclasts by sample, sector of the valve, taphonomic attribute, and its category.

	San Pedro 2008				San Pedro 2016				San Pedro 2018			
	0	1	2	abs	0	1	2	abs	0	1	2	abs
umbo												
fragmentation	178	14	13	18	245	47	14	12	194	53	19	37
periostracum	0	3	202	18	1	3	302	12	1	9	256	37
corrasion	0	5	200	18	0	6	300	12	3	20	243	37
anterior												
fragmentation	152	47	12	12	246	44	17	11	204	62	14	23
periostracum	2	18	191	12	8	23	276	11	12	23	245	23
corrasion	10	18	183	12	2	14	291	11	8	22	250	23
center												
fragmentation	148	58	11	6	265	36	14	3	192	94	13	4
periostracum	2	24	191	6	9	22	284	3	12	25	262	4
corrasion	5	29	183	6	3	13	299	3	8	22	269	4
posterior												
fragmentation	134	40	23	26	249	30	23	16	187	47	25	44
periostracum	5	15	177	26	11	20	271	16	15	20	224	44
corrasion	8	20	169	26	4	13	285	16	8	21	230	44
abs= absent												

RESULTS

The frequencies of the taphonomic attributes are presented in Figure 3; the results of the X^2 , Bonferroni, and Kendall tests are summarized in Tables 2–5.

The 2018 specimens had the lowest percentages of lost sectors (Tab. 2). Regarding the percentages, the central sector was the most represented, with a peak in 2008. The less frequent was the posterior one. The Kendall test (Fig. 4; Tab. 3) indicated that there is no correlation between lost sectors and damage by sector with time. The X^2 and Bonferroni tests (Tab. 2) showed that the umbonal and posterior sectors are differently represented, with 2008 being the distinct sample in both cases. Meanwhile, the central and anterior sectors did not exhibit differences.

Table 4 shows the frequency of taphonomic attributes. Fragmentation exhibited statistically significant differences in all sectors except the anterior over the years. In

the umbonal sector, statistically significant differences were observed in 2008 and 2018. Significant differences were also noted in the central sector for 2016 and 2018, and in the posterior sector for 2016.

Periostracum damage had no statistically significant differences in sectors or years. Category 2 was most represented in more than 85% of the bioclasts, followed by categories 1 and 0.

Corrasion was statistically different among the three samples. The distinct sample in the umbo was 2018, in the anterior 2016, in the center 2008 and 2016, and in the posterior 2016. Category 2 was represented in more than 80% of the bioclasts, followed by 1 and 0.

Category 0 was by far the most represented in all years and sectors, accounting for 88% or more of the bioclasts, followed by categories 1 and 2 in descending order. The X^2 and Bonferroni tests (Tab. 5) show that 0 was statistically

TABLE 2 – Valve sectors. χ^2 squared and Bonferroni post hoc tests, and Kendall's tau.

	umbo		anterior		center		posterior	
X²	15.122		51.426		27.895		21.761	
p (no assoc.)	0.00052		0.07643		0.24789		1.88E-01	
Bonferroni p (no assoc.)								
	umbo		anterior		center		posterior	
	pres	abs	pres	abs	pres	abs	pres	abs
2008	1	1	1	1	0.62352	0.6235	0.29792	0.29792
2016	0.00301*	0.00301*	0.28534	0.28534	1	1	0.02795*	0.02795*
2018	0.00354*	0.00354*	0.24213	0.24213	1	1	1.87E-01*	1.87E-01*

abs= absent; pres= present; *= statistically significant at 0.05%

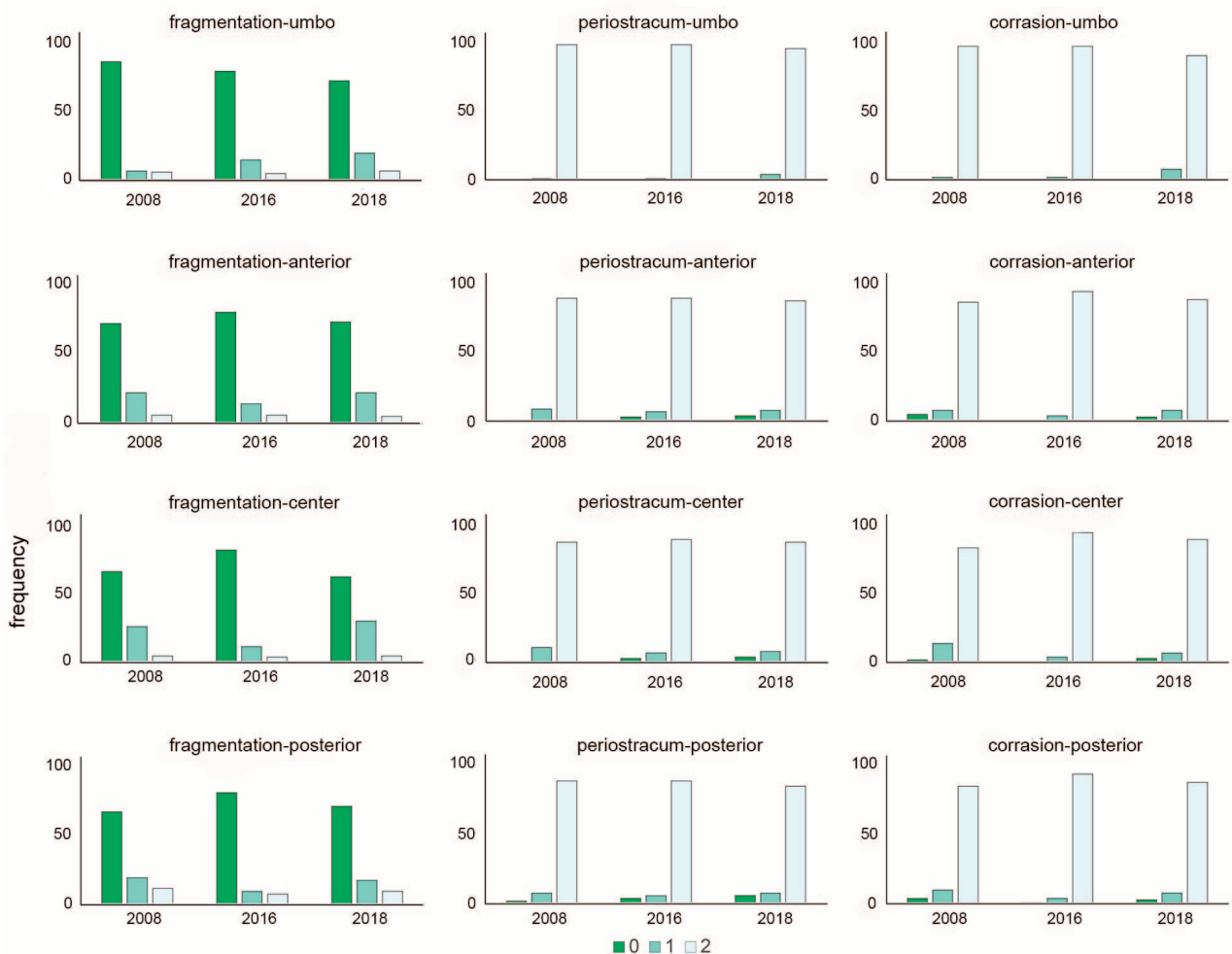


Figure 3. Frequency of taphonomic attributes over time by category, valve sector, and sample.

TABLE 3 – Kendall's tau for lost sectors, damage by sector, and taphonomic category.

	Lost sectors	Damage by sectors		Taphonomic category
	All cases	Umbo, anterior, center	Posterior	All cases
tau	0.33333	0.33333	-1	0.33333
p (uncorr.)	0.60151	0.60151	0.11719	0.60151

TABLE 4 – Frequency of taphonomic attributes by sector. X² squared and Bonferroni post hoc tests.

Fragmentation			Periostracum				Corrasion		
Umbo									
X²	18.207			54.039			19.234		
p (no assoc.)	0.00112			0.2483			0.00071		
Anterior									
X²	76.917			52.414			13.215		
p (no assoc.)	0.10355			0.26341			0.01027		
Center									
X²	39.039			69.996			18.494		
p (no assoc.)	<0.000001			0.13591			0.00099		
Posterior									
X²	16.085			36.297			11.007		
p (no assoc.)	0.00291			0.45843			0.02649		
Bonferroni p (no assoc.)									
Fragmentation			Periostracum				Corrasion		
0	1	2	0	1	2	0	1	2	
Umbo									
2008	0.01975*	0.01975*	1	1	1	1	1	1	1
2016	1	1	1	1	1	1	1	0.17866	0.07189
2018	0.01151*	0.02546*	1	1	0.30326	0.27664	0.14543	0.00259*	0.00024*
Anterior									
2008	1	1	1	0.55181	1	1	0.13988	1	0.17644
2016	0.13416	0.05418	1	1	1	1	0.07234	0.44746	0.01585*
2018	1	1	1	0.47224	1	1	1	1	1
Center									
2008	0.53244	0.67096	1	0.48408	1	1	1	0.00246*	0.00403*
2016	6.67E-04*	1.15E-04*	1	1	1	1	0.99678	0.02277*	0.00464*
2018	0.00034*	5.85E-01*	1	0.90724	1	1	1	1	1
Posterior									
2008	0.06027	0.25101	1	1	1	1	1	0.49289	0.1298
2016	0.00151	0.00581*	1	1	1	1	0.59603	0.12651	0.01626*
2018	1	1	1	0.79481	1	1	1	1	1

*= statistically significant at 0.05%

TABLE 5 – Damage by taphonomic category. χ^2 and Bonferroni post hoc tests.

χ^2	60.908		
p (no assoc.)	<0.000001		
	Bonferroni p (no assoc.)		
	0	1	2
2008	1	0.083632	1
2016	0.044167*	2.4639E-13*	0.23789
2018	0.51034	6.6107E-07*	0.89604

*= statistically significant at 0.05%

significant in the 2016 sample, and 1 in the 2016 and 2018 samples. The Kendall test (Tab. 3) indicated that there is no correlation between taphonomic categories with time.

The average taphonomic score was nearly identical across the three samples, differing only in the third decimal (2008 = 1.3658; 2016 = 1.3612; 2018 = 1.3641) (Fig. 4).

DISCUSSION

Preservation

In general, the taphonomic attributes observed in *C. fluminea* showed scarce variability, as depicted by the three samples studied. The χ^2 tests revealed statistically significant differences in the sectors represented and fragmentation, but there is no linear tendency over the years.

The central valve sector was the most frequent in the samples, while the posterior one was the least frequent. The causes seem to be morphological. The central sector is the most protected against fragmentation due to its topological position, and the valve is not too convex to form an abrasion pattern, such as in the whorls of a gastropod.

Regarding the posterior area and considering the entire molluscan death assemblages of the Touro Passo River in southern Brazil, Kotzian & Simões (2006) found that the most fragmented sector was the posterior one, as in our case. Unfortunately, it was not provided data discriminated by species. We suggest that, again, morphology is the root of this pattern. The posterior area of the *C. fluminea* shell is larger and slightly thinner than the anterior area, and as a result, it is more fragile against mechanical efforts. Newell *et al.* (2007) stated that in *Unio*, the umbo is the tallest and

most exposed zone to particle impact, and consequently, the first to be abraded, and subsequently more prone to fragmentation. As seen above, this is not the case for *C. fluminea*. This can be attributed primarily to the different morphology of both species. Newell *et al.* (2007) noted that the umbonal cavity in their *Unio* specimens was very thin and prone to abrasion and perforation, which notably favored the occurrence of fractures. This is not the case for *C. fluminea*, which has a rather thick umbonal part of the shell. The microstructure of both types of shells is also different and may play a role in the distinct preservation styles observed. Unionid shells are aragonitic, with an outer prismatic layer and an inner nacreous layer, which comprise most of the shell thickness (Checa & Rodríguez-Navarro, 2001, and references). However, the shell of *Corbicula fluminea*, which is also aragonitic, comprises three layers,

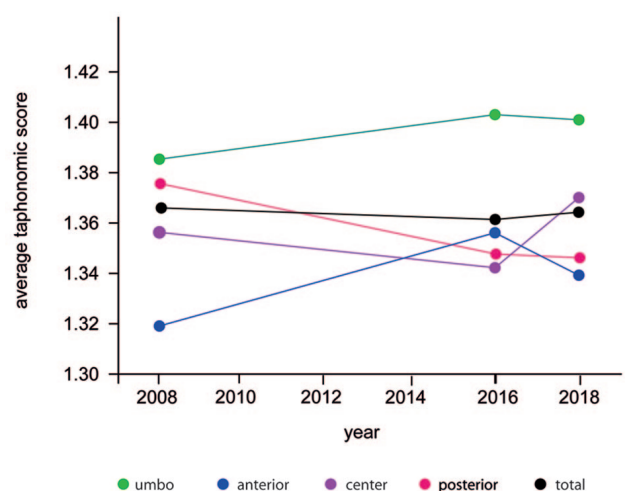


Figure 4. Average taphonomic scores over time.

from the outer to the inner: crossed-lamellar, prismatic (pallial myostracum), and complex crossed-lamellar (Fritz *et al.*, 2022, and references).

In addition, the usual low energy of the river in the study area and the absence of bioerosion may also explain the scarce fragmentation in general. The absence of bioerosion and bioencrustation reflects the low-salinity conditions in which *C. fluminea* lives. It is very improbable to find these structures in freshwater conditions (Kotzian & Simões, 2006; Tietze & De Francesco, 2014).

Worldwide, *Corbicula* species have various predators that break the shells, such as fish, birds, and crabs (Robinson & Wellborn, 1988; Cadée, 2003; Cadée & Soes, 2004; Pla Ventura *et al.*, 2018; Sanders & Mills, 2022; Kroboth *et al.*, 2024), but predation on *Corbicula fluminea* has not been yet studied in the study area.

Corrasion exhibits differences among the years: the statistically significant ones are 2018 in the umbonal sector, 2016 and 2018 in the central sector, and 2016 in the anterior and posterior sectors. In all cases, category 2 was the predominant one. The high chemical dissolution present in freshwater and estuarine conditions may not infrequently erase the eventual accumulation of taphonomic signals (Tietze & de Francesco, 2014). This is not the case, but it is interesting to note the presence of dissolution pits in some specimens (although their frequency was not quantified).

Specifically, the periostracum is the first barrier against abrasion and corrosion (Taylor & Kennedy, 1969; Harper, 1997, among others), and a correlation between periostracum loss and corrasion (specifically corrosion) has been noted (*e.g.*, Pereira *et al.*, 2021, and references). In our case, although category 2 predominates in both attributes, their distribution over the years and sectors is not linearly correlated.

Contrary to our findings, Kotzian & Simões (2006) reported small levels of corrasion for the mollusks of the Touro Passo Stream. Still, since they did not discriminate among species, their results and ours are hardly comparable. However, a different time of exposure to the taphonomic agents and/or the differing sedimentary environments of both studies (river vs. fluvial beach) may also contribute to the observed taphonomic patterns.

On the contrary, Kusnerik *et al.* (2020) found intense taphonomic damage in *Melanoides tuberculata*, an invasive gastropod that has been present in their study area (spring-fed river systems in Florida, USA) for approximately 50 years.

As stated earlier, Martínez *et al.* (2020b), Antuña *et al.* (2021), and Gómez *et al.* (2023) have pioneered studies on the taphonomy of the invasive gastropod *Rapana venosa*. In this case, they also found a pattern of early damage comparable to those shown by the Holocene or even Pleistocene mollusks from the area in this study. Comparing the taphonomic features of the shells of this species and *C. fluminea*, the primary difference is that the *R. venosa* shells underwent a considerably more intense fragmentation. This can be attributed to the presence of bioerosion structures, which weaken the shell, and to the higher energy of the environment. Both species share a high corrasion pattern, which, in the case of *R. venosa*, was attributed to physical factors (high energy). In *C. fluminea*, the principal factor may be chemical, such as the low pH of the water.

Time averaging

Other actualistic studies on shell ages and taphonomic conditions have previously concluded that the latter cannot be regarded as a straightforward indicator of age (*e.g.*, Flessa *et al.*, 1993), but the decadal time-lapse was only investigated in the latest years (Kusnerik *et al.*, 2020; Martínez *et al.*, 2020b; Antuña *et al.*, 2021; Gómez *et al.*, 2021, 2023). Specifically, regarding *C. fluminea*, Gómez *et al.* (2021) demonstrated that specimens with substantial taphonomic modifications coexist with scarcely modified exemplars after nearly four decades.

In the present work, we evaluated shells sampled apart by a decade and by only two years, and we did not find a temporal trend. For example, taphonomic damage to the shells is not more severe over time. There is no statistically significant difference when comparing samples separated by ten years with those separated by only two years. In other words, the older samples are globally as damaged as the younger ones. Then, taphonomic damage emerged very early, especially in terms of periostracum loss and corrasion. Moreover, fragmentation did not increase over the years.

At least two hypotheses can explain this situation. One

is that the specimens are not replaced in the sampling area, and thus, the taphonomic characteristics are acquired early after death, and in the following years, there are no notable modifications of the shells. The second hypothesis is that there is a partial or total replacement of the shells in the study area, and we are dealing with assemblages partially or totally composed of new shells. In this case, the assemblage would be (partially or totally) rejuvenated or reset, *i.e.*, including shells that have been exposed to taphonomic agents for a very short time, and we are recovering dissimilarly aged shells over the years (mainly). The data seem to better support the idea that shells are rapidly altered after death and that no substantial rejuvenation occurs over time. Even if there were partial or total replacement of the assemblage, we would expect to see at least some shells with better-preserved features, such as the periostracum. However, its consistent absence across samples suggests that this component is quickly lost post-mortem, and therefore, the shells observed—even if newly deposited—are already in an advanced stage of taphonomic alteration. This supports the idea that taphonomic changes occur rapidly and that the assemblage remains relatively stable in its overall condition.

We sampled without replacement, and in consequence, these shells were removed from the system, modifying the future universe of available specimens. Nevertheless, we consider that the magnitude of the alteration in such a big area with a considerable number of available shells is negligible. In any case, the conclusion regarding very early after-death taphonomic damage, in terms of periostracum loss and intense corrosion, remains unchanged. The taphonomic characteristics of the older and younger samples are very similar.

CONCLUSIONS

Within a maximum period of 36 years, the most prominent taphonomic attributes in the shells of *C. fluminea* were periostracum loss and corrosion, which followed similar trends, as expected due to the loss of the protective function of the periostracum. Surface shell modifications in *C. fluminea* in the study area are interpreted as being more chemically induced than mechanically induced.

Fragmentation was not an important taphonomic

attribute in this inner Río de la Plata fluvial beach, which is typically exposed to a low-energy regime.

Beyond the details of this research, taphonomic alterations in this freshwater environment are recognized in a short time-lapse, not exceeding 36 years, which has interesting consequences for the interpretation of fossil and death assemblages.

Comparing the taphonomic features of the shells of *C. fluminea* with previous studies on the estuarine invasive gastropod *Rapana venosa*, the most notable difference is that the shells of this species suffered considerably more intense fragmentation. This can be attributed to equally intense bioerosion and the higher energy of the environment.

ACKNOWLEDGEMENTS

Ernesto Brugnoli, Fernando Erthal, and Alvar Carranza made important suggestions when evaluating the MSc. Thesis of MCG, from which this article stems. Matias Ritter and an anonymous reviewer provided insightful advice. We thank the dedication of the Editor Gabriela Hassan. ANII (Project FCE_1_2017_1_135699) funded a scholarship for MCG and, in collaboration with PEDECIBA-Geociencias, provided financial support for this research.

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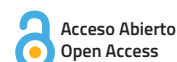
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doi: 10.5710/PEAPA.16.07.2025.538

Recibido: 4 de enero de 2025

Aceptado: 16 de julio de 2025

Publicado: 20 de octubre de 2025



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WHO EATS THE ARMADILLOS? NEOTAPHONOMY OF ACCUMULATIONS PRODUCED BY THE CROWNED EAGLE (*BUTEOGALLUS CORONATUS*)

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Abstract. Neotaphonomic studies of vertebrates provide information about the mechanisms and processes that can modify the original characteristics of skeletal elements and can be used as analogues for interpretations on the origin of archeological and paleontological assemblages. The neotaphonomic evaluation of non-ingested bones (leftover prey remains) and modified digested bones by the crowned eagle (*Buteogallus coronatus*, Accipitriformes, Accipitridae) is presented. Bones were recovered from the nests located in the central-west La Pampa Province, Argentina. Leftover prey remains include representatives of Aves, Iguania, Ophidia, Cingulata, Lagomorpha, and Carnivora. Bones from pellets correspond to Ophidia, Rodentia, and osteoderms of two armadillos Chlamyphoridae (Xenarthra, Cingulata). Some of the latter correspond to pichi (*Zaedyus pichiy* Euphractinae), a common species that is usually located in the diet of *B. coronatus*. *Zaedyus pichiy* osteoderms, recovered from pellets, present modifications in the original ornamentation, as well as a reduction in their thickness. Various pellets also contained remains of the pink fairy armadillo (*Chlamyphorus truncatus*, Chlamyphorinae), a small paradigmatic, nocturnal and fossorial species, endemic to central-western Argentina, which is recorded for the first time as part of this raptor diet. This first mention of *Chl. truncatus* being captured by the crowned eagle is relevant because it involves two little-known and sympatric species, in an area where this armadillo is endemic. Osteoderms of *Chl. truncatus* show an extreme degree of modification, and it is interpreted that its potential of preservation in the fossil record is very low.

Key words. Actualistic taphonomy. Accipitridae. Chlamyphoridae. Digested osteoderms. Central-western Argentina.

Resumen. ¿QUIÉN SE COME A LOS ARMADILLOS? NEOTAFONOMÍA DE ACUMULACIONES PRODUCIDAS POR EL ÁGUILA CORONADA (*BUTEOGALLUS CORONATUS*). Los estudios neotafonómicos de vertebrados proveen información sobre los mecanismos y procesos que pueden modificar las características originales de los elementos esqueléticos de vertebrados actuales, y pueden usarse como análogos para interpretar el origen de asociaciones arqueológicas y paleontológicas. Se presenta la evaluación tafonómica de restos óseos no ingeridos (restos de presa) y huesos digeridos modificados, procedentes de egagrópilas del águila coronada (*Buteogallus coronatus*, Accipitriformes, Accipitridae). Los materiales proceden de nidos ubicados en el centro-oeste de la provincia de La Pampa, Argentina. Los restos de presa incluyen representantes de Aves, Iguania, Ophidia, Cingulata, Lagomorpha y Carnivora. Los huesos contenidos en las egagrópilas corresponden a Ophidia, Rodentia y osteoderms de dos armadillos Chlamyphoridae (Xenarthra, Cingulata). Parte de los osteoderms recuperados se asignaron a *Zaedyus pichiy* (Euphractinae), una especie común que habitualmente está presente en la dieta de *B. coronatus*. Los osteoderms de *Zaedyus pichiy*, recuperados de egagrópilas, presentan modificaciones en la ornamentación original y una reducción de su espesor. Varias egagrópilas también contenían osteoderms del pichiciego *Chlamyphorus truncatus* (Chlamyphorinae), un pequeño y paradigmático armadillo nocturno y fosorial, endémico del centro-oeste de la Argentina, que se registra por primera vez como parte de la dieta de esta ave rapaz. Esta primera mención de *Chl. truncatus* como parte de la dieta del águila coronada es relevante porque involucra dos especies simpátricas y poco conocidas, en un área donde este armadillo es endémico. El grado de modificación de los osteoderms de *Chl. truncatus* es extremo, por lo que se interpreta que su potencial de preservación en el registro fósil es muy bajo.

Palabras clave. Tafonomía actualística. Accipitridae. Chlamyphoridae. Osteoderms digeridos. Centro-oeste de Argentina.

ACTUALISTIC TAPHONOMY or neotaphonomy (Tedford, 1970; Lyman, 1994) of vertebrates is becoming frequent, particularly those studies focused on the predator–prey interaction (Lyman, 2018), as they provide valuable information about the mechanisms and processes that can modify the original characteristics of skeletal elements (Lyman, 1994). These kinds of studies can be used as analogues for interpretations on the origin of both archeological and paleontological assemblages (Fernández–Jalvo & Andrews, 1992; Fernández *et al.*, 2017; Montalvo & Fernández, 2019).

In this contribution, we perform a neotaphonomic study on a central arid and semi-arid region of Argentina, which corresponds to the southern portion of the Central or Subandean Zoogeographic Domain (Ringuet, 1961). This region is known for hosting fossiliferous deposits from the Late Miocene–Holocene lapse (*e.g.*, Verzi *et al.*, 2008; Montalvo *et al.*, 2017, 2023) and for developing naturalistic taphonomic studies, mainly focused on predators, and conducted at a wide spatial scale (Montalvo *et al.*, 2007, 2008, 2011, 2012, 2014, 2016, 2020; Montalvo & Tallade, 2009; Fernández *et al.*, 2017, 2025; Montalvo & Fernández, 2019). In this case, we analyzed the prey–remains of the crowned eagle *Buteogallus coronatus* (Vieillot, 1817) (Accipitriformes, Accipitridae), also called chaco eagle, from a neotaphonomic point of view. This eagle is one of the largest raptor birds in South America (body mass between 3 and 3.7 kg). It mainly inhabits open woodlands in xerophytic and humid forests typical of southern Brazil, Paraguay, eastern Bolivia, and Argentina, with its austral limit of distribution reaching northern Patagonia (Sarasola *et al.*, 2022). This raptor is mostly solitary and crepuscular, and its hunting techniques include perching and waiting for prey, as well as performing circular low-altitude flights approximately 100 m above the ground (Pereyra Lobos *et al.*, 2011). Nests are constituted by large platforms placed on top of trees composed of sticks (Maceda, 2007). *Buteogallus coronatus* has opportunistic and generalist habits. It accumulates large amounts of leftover prey remains (mainly skins, bones, and osteoderms) around the nest in open landscapes and, on some occasions, several pellets can also be recorded in the nesting area (Montalvo *et al.*, 2016; Guardia *et al.*, 2024). In particular, the diet of this

raptor primarily includes mammals, mainly Chlamyphoridae (Xenarthra, Cingulata), as well as Mephitidae and Mustelidae (Carnivora), Leporidae (Lagomorpha), Caviidae, Cricetidae, and Ctenomyidae (Rodentia), but it also consumes other vertebrates such as snakes (Elapidae, Viperidae, and Dipsadidae), tortoises (Testudinidae), lizards (Teiidae, Iguanidae), fishes, and birds (*i.e.*, Tinamidae, Psittacidae, Cracidae, and Rheidae) (Maceda *et al.*, 2003; Maceda, 2007; Chebez *et al.*, 2008; Pereyra Lobos *et al.*, 2011; Galmes *et al.*, 2018). Sarasola *et al.* (2010) also recorded the consumption of diverse insects and arachnids. There are no known fossil remains of the crowned eagle, and those of Accipitridae are scarce in Argentina.

Neotaphonomic analyses of the modifications produced by *Buteogallus coronatus* on prey remains (both digested and non–ingested) are scarce. The modifications generated by this raptor during capture and handling of diurnal Chlamyphoridae armadillos (including the Euphractinae *Zaedyus pichiy* Desmarest, 1804, *Chaetophractus villosus* Desmarest, 1804, and *Chaetophractus vellerosus* (Gray, 1865), recovered from several accumulations of prey remains in La Pampa Province (central Argentina), were studied by Montalvo *et al.* (2016). Recently, Guardia *et al.* (2024) analyzed non–ingested vertebrate leftover prey remains accumulated by the crowned eagle in the Ñancuñán Biosphere Reserve in Mendoza Province (central–western Argentina). Montalvo *et al.* (2016) and Guardia *et al.* (2024) suggested that neotaphonomic observations can be used in subsequent studies of armadillo bone accumulations from open–air archeological or paleontological sites from central Argentina and other parts of South America inhabited by this eagle, as well as in future revisions of samples.

The IUCN listed the crowned eagle as a vulnerable species until 2004, when it was declared endangered (BirdLife International, 2024). Many aspects of its biology and ecology are still unknown, including habitat use and dispersal behavior (Sarasola *et al.*, 2022). Considering this situation, all the information obtained from the study of the ingested or handling remains during its feeding is considered of particular interest.

Chlamyphoridae (Cingulata) representatives are noteworthy among the prey of *Buteogallus coronatus*. This group of ‘armored’ xenarthran mammals are characterized by

having a protective carapace composed of ossified dermal tissues known as osteoderms (Gaudin & McDonald, 2008). Recent phylogenetic data strongly support the monophyly of four armadillo subfamilies gathered into two families: Dasypodinae (long-nosed armadillos) within Dasypodidae and Euphractinae (hairy, six-banded, and pichi armadillos), Tolypeutinae (three-banded, naked-tailed, and giant armadillos), and Chlamyphorinae (pink fairy armadillos) within Chlamyphoridae (Delsuc *et al.*, 2012, 2016; Gibb *et al.*, 2016; Barasoain *et al.*, 2020).

Within Chlamyphorinae, *Chlamyphorus truncatus* Harlan, 1825, commonly named as pink fairy armadillo and 'pichiciego', represents the smallest armadillo and one of the most bizarre, elusive, and unknown living mammals (Minoprio, 1945; Barasoain *et al.*, 2020). It is a nocturnal and fossorial species with solitary habits, endemic to the Central or Subandean Zoogeographic Domain of Argentina (Borghi *et al.*, 2011). This species inhabits dry grasslands and sandy plains with shrubby vegetation along the following ecoregions: Monte of plains and plateaus, Espinal, arid Chaco, Monte of hills and valleys, and Pampas grassland (Abba *et al.*, 2012). *Chlamyphorus truncatus* has a diet mainly composed of insects (such as ants and beetles), worms, snails, and small amounts of roots and other plant parts (Borghi *et al.*, 2011). However, the biology, ecology, and evolutionary history of *Chl. truncatus* is poorly known, fundamentally due to their lifestyle. In addition, there are no publications on the specific physiological adaptations of this armadillo to inhabiting extreme areas such as the xeric environments (Superina *et al.*, 2014). Representatives of the subfamily Chlamyphorinae were recovered from Late Miocene levels of the Cerro Azul (La Pampa and Buenos Aires provinces) and Loma de las Tapias (San Juan Province) formations (Barasoain *et al.*, 2020). Some specimens described for the Late Pleistocene (Buenos Aires Province) and Holocene (San Luis Province) were discussed by Scillato-Yané (1982). At the moment, there is an absence of fossil chlamyphorines between the Late Miocene to the present.

The pichi, *Zaedyus pichiy*, is an Euphractinae that represents an important item of *Buteogallus coronatus* diet (Sarasola *et al.*, 2022). In Argentina, skeletal elements of this armadillo were recovered as leftover prey remains in different nests from La Pampa and Mendoza provinces with

the objective of carrying out neotaphonomic evaluations (Montalvo *et al.*, 2016; Guardia *et al.*, 2024). It is a relatively small (*ca.* 1 kg), solitary and diurnal animal that lives in arid and semi-arid habitats in central and southern Argentina and Chile (Wetzel, 1985), reaching altitudes up to 2,500 m. In Argentina, it inhabits different ecoregions: Patagonian Steppe, Monte of plains and plateaus, Pampas grassland, and Espinal (Abba *et al.*, 2012). This species is currently listed as near threatened by the IUCN Red List of Threatened Species (Superina & Abba, 2014). The present-day diversity of Euphractinae is restricted to three genera, having been considerably greater in the past. With respect to the fossil record, remains assigned to *Zaedyus* were mentioned for the Late Miocene of the Ituzaingó Formation (Entre Ríos Province, Argentina) (Scillato-Yané *et al.*, 2013). However, reliable remains of *Z. pichiy* are known since the Early to Middle Pleistocene in the Pampean region (Soibelzon *et al.*, 2010). Holocene archeological records of this species are known in the Pampean region.

In the context of the neotaphonomic evaluation carried out here on pellets and leftover prey remains produced by *Buteogallus coronatus* in La Pampa Province, digested osteoderms of *Zaedyus pichiy* were recovered from pellets, and non-ingested bones (mainly carapace portions) were recovered from nest, while digested osteoderms of *Chlamyphorus truncatus* were identified only in pellets. We analyze and interpret the modifications generated by digestion on both armadillo osteoderms and different skeletal elements from other vertebrates. This study provides novel information on the trophic interaction between *B. coronatus* and two species of Chlamyphoridae in central Argentina, contributes to improving knowledge about their ecology, and represents the first evidence of *Chl. truncatus* as part of the crowned eagle diet.

PHYTOGEOGRAPHIC, BIOGEOGRAPHIC AND CLIMATIC CHARACTERIZATION

From a phytogeographic viewpoint, the materials evaluated (pellets and leftover prey remains) were recovered from two ecoregions in La Pampa Province, Argentina: the Espinal and the Monte Desert (Cabrera, 1994) (Fig. 1.1). The Espinal, in the central sector of the province, corresponds to the Caldén District, characterized by xeric deciduous

forests, mainly caldén [*Neltuma caldenia* (Burkart, 1939)], as well as clearings covered by very open to park-type grassy savannas, and dunes and salty soils. In the dune areas, scrublands and sammophilous grassland develop (Oyarzabal *et al.*, 2018). In the western sector of the province, the vegetation of the Monte Desert is represented by a high shrub steppe, characterized by communities of *Larrea* spp. with isolated caldén trees. In the area of the Atuel–Salado–Chadileuvú wetlands, a low shrub steppe stands out with halophytic scrub (Oyarzabal *et al.*, 2018).

Both ecoregions share a diverse fauna of terrestrial vertebrates, although their frequency of appearance varies between areas. These vertebrates are usually prey of *Buteogallus coronatus* (Chebez *et al.*, 2008; Sarasola *et al.*, 2010; Pereyra Lobos *et al.*, 2011). Among reptiles, species include Testudinidae, Teiidae, Liolaemidae and Viperidae, Colubridae, Elapidae (Bauni *et al.*, 2021). Birds include the Rheidae, Tinamidae, Columbidae, Tytonidae, and a great diversity of Passeriformes families (Verga *et al.*, 2019). Mammals are represented by Didelphidae; Chlamyphoridae Euphractinae and Chlamyphorinae; rodents such as Octodontidae, Ctenomyidae, Caviidae, Chinchillidae, and Cricetidae; Camelidae, and several Carnivora as Felidae, Mustelidae, Mephitidae, and the Canidae (Soibelzon *et al.*, 2021).

Climate is temperate in both ecoregions, with an average annual temperature ranging from 14°C and 16°C and a marked thermal amplitude (around 16°C), more pronounced

towards the west. Maximum summer temperatures range from 40°C to 45°C, while winter minimums range from -17°C to -10°C. The scarce rainfall ranges from 80 to 300 mm per year in the Monte Desert and from 300 to 550 mm per year in the Espinal (Cabrera, 1994).

MATERIALS AND METHODS

We evaluated the vertebrate remains obtained from 43 pellets and non-ingested leftover prey remains produced by *Buteogallus coronatus*, which were recovered from different nests areas located in the Espinal and Monte desert of La Pampa Province (Fig. 1.2–3; Tab. 1). Both pellets and leftover prey remains samples (Tab. 1) were collected during 2012 and 2013. They were found on the surface of the substrate, around the bases of the trees where the nests were located; most of the findings correspond to accumulations of leftover prey remains. Details of leftover prey remains were previously evaluated from a taxonomic and neotaphonomic perspective by Montalvo *et al.* (2016). The materials studied are housed in the Vertebrate Collection from FCEN, UNLPam.

Pellet collection was carried out in the field under conditions as undisturbed as possible. Posteriorly, they were broken down dry and the bones were extracted under laboratory conditions. These remains were classified and examined using a stereo microscope Leica MS5. Photographs were taken with a Nikon d3100 camera and some osteoderms were photographed under a scanning

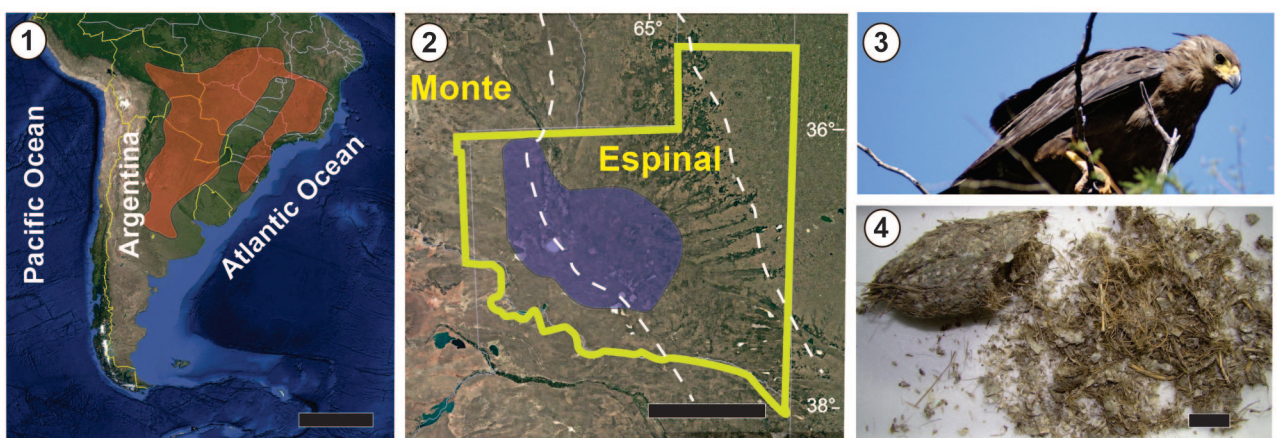


Figure 1. *Buteogallus coronatus*. 1, Distribution in South America in red; scale bar= 1000 km; 2, In blue, area of localities in La Pampa Province (see Tab. 1), and different ecoregions of this province; scale bar= 160 km; 3, Photograph of *B. coronatus*; 4, Portions of complete and disaggregated pellets; scale bar= 10 mm. Images 1–2 from Landsat/Copernicus 2023; Google Earth, accessed December 2023.

electron microscope ZEISS GeminiSEM 360 at Instituto de Ciencias de la Tierra y Ambientales de La Pampa (CONICET–UNLPam).

Taxonomic identifications are based on comparison with current specimens from the vertebrate collections of the FCEN, UNLPam (MKUNLPam) and MPH–ZM. Following Badgley (1986), we calculated the number of identified specimens per taxon, the MNE, and the MNI from each pellet and from the whole sample (including the non-ingested leftover prey remains).

For the neotaphonomic evaluation of the scarce rodent remains, we partly followed the standard methodology of Andrews (1990), Fernández–Jalvo & Andrews (1992), Fernández *et al.* (2017), and Montalvo & Fernández (2019). This methodology allows categorizing predators using several characteristics: the relative abundance of skeletal elements, considering the MNEi as a function of the expected number of that specific skeletal Ei and the MNI, after $MNEi/(Ei \times MNI) \times 100$; calculation of indexes of element proportion: $[(\text{humerus} + \text{femur}) / (\text{mandible} + \text{maxilla})] \times 100$ and $[(\text{tibia} + \text{radius}) / (\text{femur} + \text{humerus})]$; corrosion marks produced by digestive acids on the surfaces of incisors,

molars, and postcranial elements; and breakage of skulls, mandibles, and postcranial elements.

Remains of *Zaedyus pichiy* and *Chlamyphorus truncatus* recovered from pellets consist mainly of isolated osteoderms from different portions of the armor. The neotaphonomic methodology used is that proposed by Tomassini *et al.* (2023), who analyzed breakage degree and type of fractures; modifications of articular and broken edges; modifications of the surface (including desquamation or exfoliation of bone layers); and modifications of original ornamentation patterns. In order to evaluate the representativeness of the digested osteoderms of *Z. pichiy*, they were evaluated in relation to the total number of osteoderms present in a complete carapace, using data from Montalvo *et al.* (2016). The total number of osteoderms present in a complete dorsal carapace of *Chl. truncatus* (including scapular and pelvic shields, and mobile rows) and the number of osteoderms in each of them were counted in 11 taxidermied individuals (vertebrate collections of FCEN, UNLPam and MPH–ZM).

Snake remains recovered from the pellets are mainly represented by several ribs, segments of the vertebral

TABLE 1 – Different nest localities of *Buteogallus coronatus* evaluated in this study (see Fig. 1.2), geographic coordinates, ecoregion (*sensu* Cabrera, 1994), number of pellets and leftover prey remains recovered.

Localities	Latitude (S)	Longitude (W)	Ecoregion	Pellets	MNI* of leftover prey Chlamyphoridae**	MNI* of other vertebrate leftover prey remains
San José	36°37'3.19"	65°42'12.88"	Espinal	2	50	1 <i>Patagioenas picazuro</i>
Las Nutrias	36°45'36.52"	65°41'8.43"	Espinal	1	10	-
San Eduardo	36°52'46.42"	65°39'59.69"	Espinal	1	13	-
El Piolín	37°11'25.53"	65°41'54.53"	Espinal	1	-	-
Don Rodrigo	36°45'35.20"	65°50'43.88"	Espinal	4	-	1 <i>Galictis cuja</i>
Campomar	36°49'30.53"	65°59'10.47"	Espinal	1	14	1 <i>Lepus europaeus</i>
El Odre	36°55'59.22"	66°10'25.47"	Espinal	2	-	-
Torres	36°04'05.50"	66°39'34.10"	Monte Desert	1	19	1 <i>Conepatus chinga</i>
Ventrecó	36°37'34.40"	66°53'20.00"	Monte Desert	3	37	2 <i>Micrurus pyrrhocryptus</i> 1 <i>Salvator</i> sp.
El Tres	36°51'02.20"	66°47'57.00"	Monte Desert	1	22	-
Vicente	36°55'30.00"	66°43'36.43"	Monte Desert	25	20	-

*MNI Minimum number of individuals; **Data from Montalvo *et al.* (2016a) and this work.

column, and isolated vertebrae. In some cases, portions of the skeleton are covered with scales (smooth or keeled) that facilitated their taxonomic assignment. Bird remains are very scarce, both in the pellets and leftover prey remains, which prevented their taxonomic identification, as well as a detailed neotaphonomic evaluation. In each case, the recovered skeletal elements were analyzed considering completeness, type of fractures, and possible marks produced by the predator.

Institutional abbreviations. FCEN, UNLPam, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, La Pampa, Argentina; MPHn–ZM, Museo Provincial de Historia Natural–Zoología Mamíferos, La Pampa, Argentina; MKUNLPam, Marta Kin collection, Universidad Nacional de La Pampa, La Pampa, Argentina.

Other abbreviations. Ei, element in the individual; IUCN, International Union for the Conservation of Nature; MNE, minimum number of elements; MNEi, representation of each element in the sample; MNI, minimum number of individuals.

RESULTS

Pellets and leftover prey remains

The location of prospected nests of *Buteogallus coronatus* is shown in Figure 1.2; the number of pellets and the minimal

number of individuals identified as leftover prey remains (both Chlamyphoridae and other vertebrate taxa) from each nest are shown in Table 1. A low number of pellets was generally found, except in the nest of Vicente locality. All the pellets contained very few bones, abundant scales of snakes, hair, feathers, and claws, as well as plant remains (Fig. 1.4). Other vertebrates, recovered as leftover prey remains, include representatives of Iguania, Ophidia, Aves, and Mephitidae, Mustelidae, and Leporidae mammals.

Vicente and Las Nutrias localities. The nest in Vicente locality provided the highest number of pellets (25); 24 with bones and one only with hair. Out of the mentioned 24, four contained bones of the caviomorph *Ctenomys* sp. and the cricetid *Eligmodontia* sp. The MNE is 169 and the MNI is 5 (*Ctenomys* sp., MNI = 2; *Eligmodontia* sp., MNI = 3), and a low average relative abundance of skeletal elements (22.11%) was obtained. However, if we only consider the pellet with the best representation of *Eligmodontia* sp. bones (MNI = 1), the average relative abundance reaches 80.53% (Fig. 2), indicating that this individual was eaten whole.

For Vicente locality, the postcranial/cranial index (= 92.63) reflects a similar representation of elements, while the [(tibia + radius) / (femur + humerus) × 100] index (= 125) shows a higher proportion of proximal elements of the limbs.

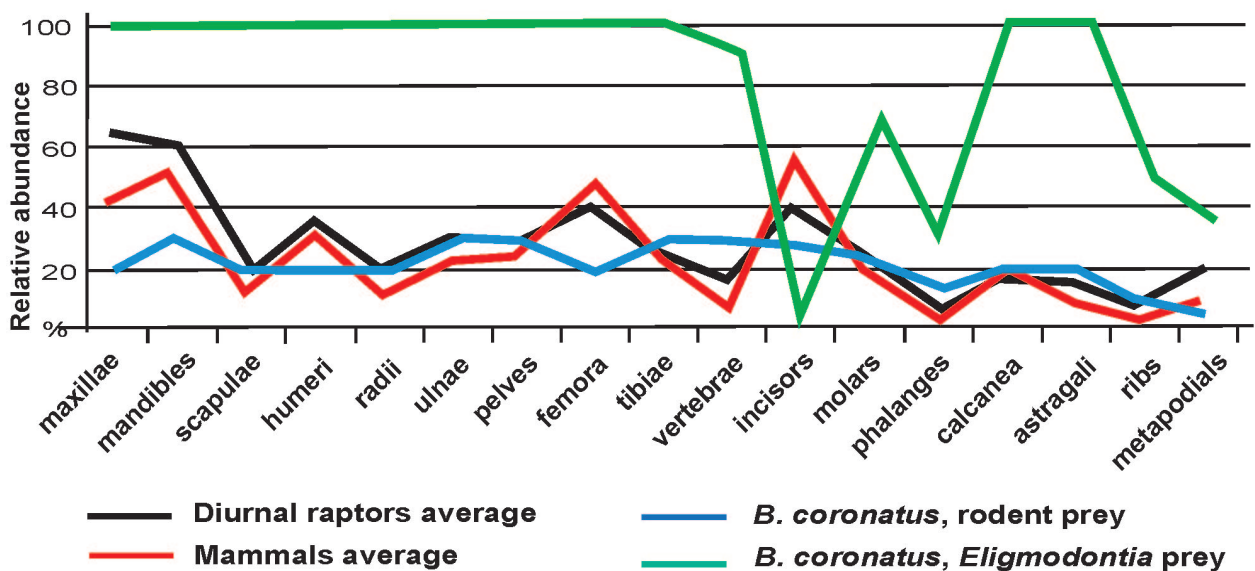


Figure 2. Relative abundance of rodent remains recovered from *Buteogallus coronatus* pellets of Vicente nest locality (in blue), compared with data from one pellet with *Eligmodontia* (in green), diurnal raptors (in black), and carnivore mammals average (in red) (data for the two latter taken from Montalvo & Fernández, 2019).

In these samples, the majority of postcranial elements (scapulae, radii, ulnae, tibiae, pelvis, and vertebrae—four of them articulated) were preserved incomplete. Cranial and mandibular elements were fragmentary, except a partially complete cranium of *Eligmodontia* sp. (Fig. 3.1, 4). Characteristics related to the digestive action were identified in five isolated incisors (three with extreme degree and two with moderate degree) (Fig. 3.2–3); seven molariforms of *Eligmodontia* sp. (Fig. 3.4) with a light digestion degree, and four molariforms of *Ctenomys* sp. (Fig. 3.5–6) with an extreme digestion degree. No evidence of digestion was identified in femora and humeri.

Six pellets of Vicente locality contained a total of 243 osteoderms belonging to *Chlamyphorus truncatus*, most of them with evidence of digestive corrosion. The assignment to this taxon was based on the morphological characteristics of the osteoderms (see below) and the presence of several typical claws of the forelimbs, which are adapted to the fossorial habit. In these pellets, one broken scapula, 15 broken ribs, 12 articulated and eight isolated vertebrae (one articulated with a rib), and eight complete phalanges were

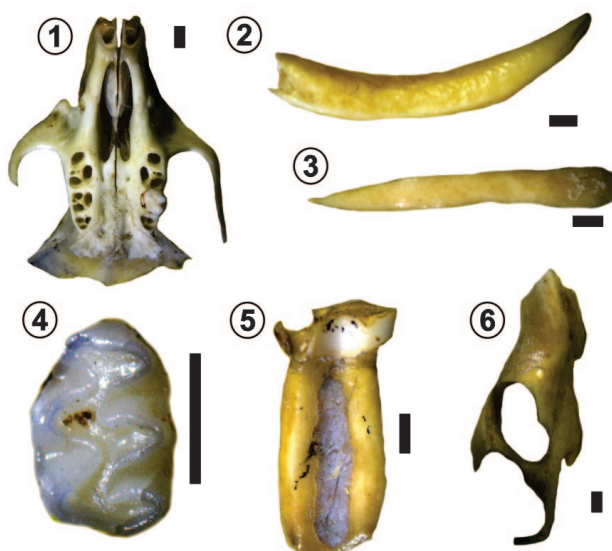


Figure 3. Rodent digested teeth and bones recovered from *Buteogallus coronatus* pellets. 1, *Eligmodontia* sp., ventral view of cranium with light digestion molar; 2–3, cricetid inferior incisors with extreme degree of digestion (lateral and ventral view, respectively); 4, *Eligmodontia* sp., occlusal view of first upper molar without digestion; 5, *Ctenomys* sp., lateral view of molar with extreme degree of digestion; 6, *Ctenomys* sp., occlusal view of portion of mandibular bone. Scale bar = 1 mm.

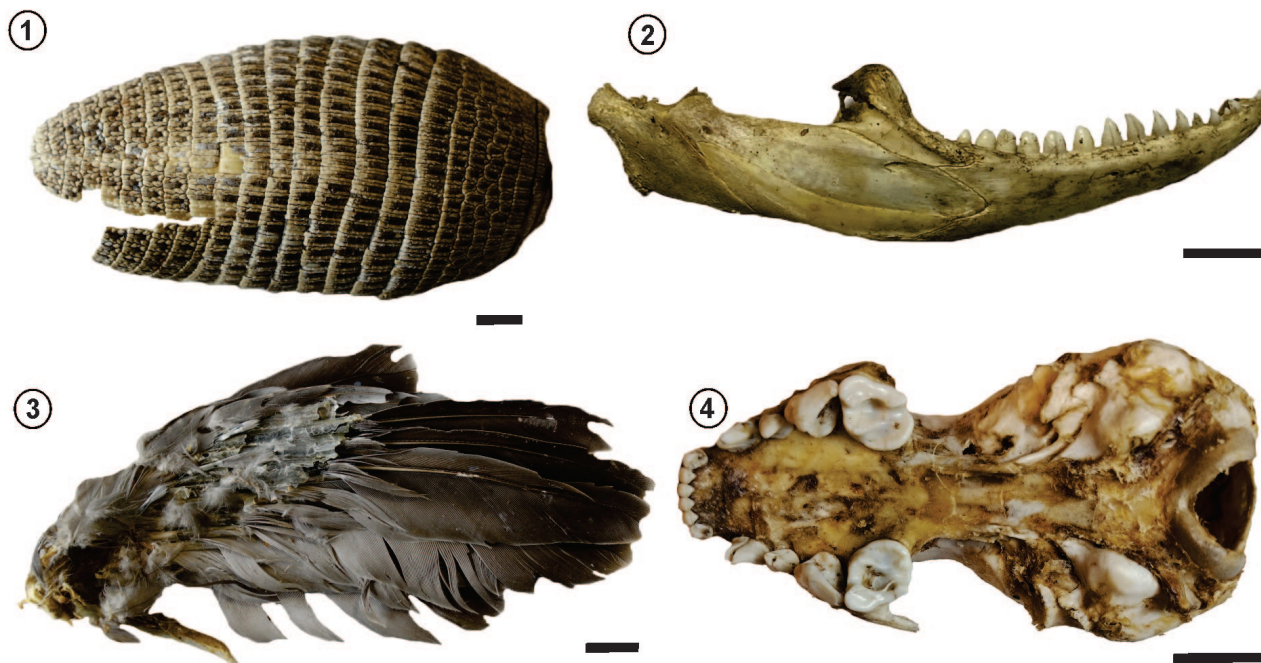


Figure 4. Leftover prey remains from different localities with signs of predation. 1, *Zaedyus pichiy*, dorsal view of carapace; 2, *Salvator* sp., lateral view of mandible; 3, *Patagioenas picazuro*, dorsal view of wing; 4, *Conepatus chinga*, ventral view of cranium. Scale bar = 10 mm.

also recovered. Regarding digestive corrosion, a light degree was recorded in seven vertebrae, two phalanges, and nine undeterminable bone fragments. These skeletal elements could only be assigned to Mammalia indet. From this nest, four pellets contained postcranial elements of *Zaedyus pichiy* (see below), including nine osteoderms. In one pellet, scales of the Patagonia green racer *Philodryas patagoniensis* (Girard, 1858) were recovered. In 10 pellets, there were several undetermined bony remains (10 diaphyses, 16 phalanges, and 26 bone fragments with light digestion).

The single pellet recovered from Las Nutrias locality contained skeletal elements of undetermined rodents, represented by one femur, five ribs, and 10 phalanges, together with six undeterminable bone fragments, all of them without evidence of digestion; and two undetermined phalanges and six vertebrae with heavy digestive corrosion. Besides, this pellet provided 77 digested osteoderms of *Chlamyphorus truncatus* and several keeled scales of the viper *Bothrops* sp.

The leftover prey remains from Vicente and Las Nutrias localities (Tab. 1) included the Euphractinae *Zaedyus pichiy* (Fig. 4.1), *Chaetophractus villosus*, and *Ch. vellerosus* with predation marks (Montalvo et al., 2016).

Don Rodrigo and Ventrencó localities. Four pellets were recovered from Don Rodrigo locality, with a total MNE of 99. Besides, one isolated vertebra, two portions of articulated vertebrae (with four and 56 vertebrae, respectively), and one cranial fragment of Ophidia indet. were recovered. There were also several scales of *Philodryas patagoniensis* and *Bothrops* sp. In one pellet, 24 digested osteoderms from the mobile bands of the dorsal carapace of *Zaedyus pichiy* were identified. A single partial cranium of *Galictis cuja* Molina, 1782 (Mustelidae, Carnivora) was recovered as a leftover prey remain (Tab. 1).

From Ventrencó locality, three pellets with scarce bone remains were recovered, including one diaphysis of Mammalia indet., two phalanges, and the left portion of maxilla with two molariforms of *Zaedyus pichiy*, all of them without evidence of digestion. As leftover prey remains (Tab. 1), two portions of articulated vertebrae and ribs of the snake *Micrurus pyrrhocryptus* (Cope, 1862) and the lizard *Salvator* sp. were recovered (Fig. 4.2). These materials added to the previously mentioned carapaces of the armadillos Z.

pichiy, *Chaetophractus villosus*, and *Ch. vellerosus* with signs of predation (Montalvo et al., 2016).

Other nest localities. San José, Campomar, San Eduardo, El Tres, Torres, El Odre, and El Piolín localities provided scarce pellets (Tab. 1) with few bony remains. Regarding mammals, materials include one molar of *Ctenomys* sp., with extreme digestion, one diaphysis with light digestion, one astragalus, and 14 phalanges. In San José, Campomar, El Piolín and El Odre localities, identified materials also include scales and vertebrae of *Philodryas patagoniensis* and *Bothrops* sp. Two vertebrae were isolated, while the others were articulated (49 assigned to *P. patagoniensis* from San José nest locality, and 68 assigned to *Bothrops* sp. from El Piolín locality). In San José locality, one pellet provided an undetermined avian bone with light digestion degree and ophidian vertebrae, 49 articulated and two isolated with light digestion degree.

In all these nest localities, portions of carapace of *Zaedyus pichiy*, *Chaetophractus villosus*, and *Ch. vellerosus* were recovered as leftover prey remains, with marks of predation (Montalvo et al., 2016). Other materials recovered as leftover prey remains (Tab. 1) include a wing with several feathers of *Patagioenas picazuro* (Temminck, 1813) (Columbiformes) in San José locality (Fig. 4.3), a cranium of *Lepus europaeus* Pallas, 1778 (Lagomorpha) in Campomar locality, and a cranium of *Conepatus chinga* Molina, 1782 (Carnivora) in Torres locality (Fig. 4.4).

Armadillos as prey

Pink fairy armadillo, *Chlamyphorus truncatus*. The geographic range of this armadillo encloses a relatively large area in central Argentina (Fig. 5.1; Superina, 2006). The carapace morphology of *Chl. truncatus* is unusual among armadillos in general. Silky white hair covers their body beneath the carapace. These characteristics are linked with its lifestyle (Superina & Loughry, 2012).

The armor (Fig. 5.2–3) is composed of a cephalic shield, continuous with the flexible dorsal carapace with a large number of mobile rows, and very reduced scapular and pelvic shields, both with fixed osteoderms, and a unique posterior structure among mammals called rump plate.

The cephalic shield is composed of five or six rows with thin, quadrangular, and fixed osteoderms covered by cornified scales (Fig. 5.2, 4; Tab. 2).

The whole dorsal carapace, from the beginning of the scapular shield to the rump plate, is connected to the body only by a median thin membrane along the spinal column. It is composed of 24 to 27 rows with a minimum of 381 and a maximum of 501 osteoderms (Fig. 5.3; Tab. 2). The different sections of the dorsal carapace (including scapular and pelvic shields, and mobile rows) are composed of successive and thin imbricated osteoderms covered by cornified scales (Krmptotic *et al.*, 2024). Each mobile osteoderm is rectangular, longer than wide, very thin (<1 mm); it has an unornamented proximal articular portion and a caudal portion ornamented with a barely raised central area surrounded laterally by slight depressions (Fig. 5.5, 7). In areas where two adjacent mobile rows connect, the osteoderms become markedly thinner (Krmptotic *et al.*, 2024, fig. 4b). Osteoderms of the scapular shield have one or two

thin glandular dorsal foramina. The osteoderms of some mobile rows from the pelvic shield generally present at its posterior margin only one piliferous foramen (sometimes two), from which a single, almost transparent hair usually emerges (Krmptotic *et al.*, 2024). Fixed osteoderms are shorter and quadrangular. Finally, the rump plate (Fig. 5.6) is composed of osteoderms mainly organized in five rows and with an average of 70 plates (minimum of 66 to a maximum of 95). The osteoderms of this plate are much thicker than those of the rest of the dorsal shield and the covering cornified scale is thin.

The sample studied contains mainly mobile osteoderms from different rows of the dorsal carapace, which show evident modifications of digestion (see below). Most osteoderms are disarticulated and have lost the cornified scale that covered them. We have identified cornified scales only

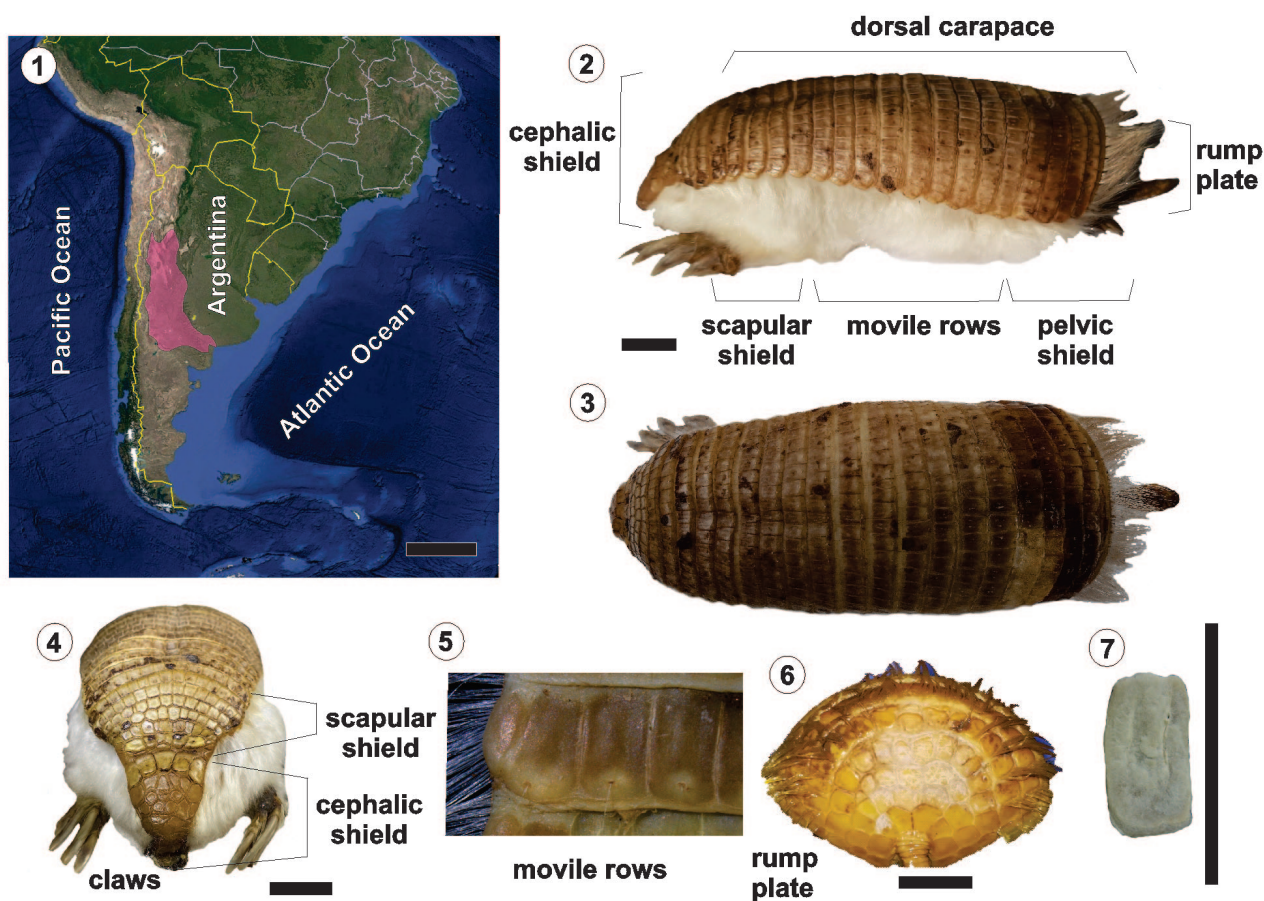


Figure 5. *Chlamyphorus truncatus*. 1, Distribution of *Chl. truncatus* in Argentina; scale bar= 1000 km; 2, Lateral view showing the different portions of the armor; 3, Dorsal view; 4, Detail of the cephalic and scapular shields in anterodorsal view; 5, Articulated osteoderms of the mobile row in dorsal shield (no scale); 6, Rump plate showing fixed osteoderms in external view; 7, Isolated osteoderm in external view. Scale bar= 10 mm for images 2–7. Image 1 from Landsat/Copernicus 2023; Google Earth, accessed December 2023.

TABLE 2 – Specimens of *Chlamyphorus truncatus* from MKUNLPam and MPHN–ZM collections with details of the different portions of the armor, used for comparison.

Specimen	Rows	Cephalic shield osteoderms	Rows	Dorsal carapace osteoderms	Rows	Rump plate osteoderms	Total osteoderms
MKUNLPam 2110	5	22	26	491	5	74	587
MKUNLPam 1003	5	26	25	381	5	73	480
MKUNLPam 1309	5	30	24	459	5	69	558
MKUNLPam 2111	6	26	26	410	6	95	531
MPHN-ZM 00826	5	27	24	418	5	70	515
MPHN-ZM 00654	6	25	23	450	5	83	558
MPHN-ZM 00824	5	22	24	442	5	67	531
MPHN-ZM 00496	6	24	24	501	5	66	591
MPHN-ZM 00966	6	30	25	425	6	92	547
MPHN-ZM 00003	6	28	27	485	5	75	588
MPHN-ZM 00971	6	29	26	486	5	84	599

in several articulated osteoderms belonging to the posterior area of the scapular shield.

In six pellets from Vicente and one from Las Nutrias localities, the number of evaluated dorsal carapace osteoderms is 317, a low value regarding the total number present in each carapace (Tab. 2). Particularly, the pellets from Vicente locality were recovered in the same date, providing 240 osteoderms. Even though this value is low, it could be reflecting that osteoderms of a single individual were incorporated in several pellets. From Vicente locality, 141 osteoderms (25.49% of the total number in one individual) were recovered from two pellets in August 2013; 37 osteoderms (6.69%) from two pellets in June 2013; and 62 osteoderms (11.21%) from one pellet in July 2012. In Las Nutrias nest locality, 77 osteoderms were recovered from one pellet in February 2012 (13.92% of the total number in one individual). These data confirm a very low representativeness of osteoderms in each pellet with significant loss of these skeletal elements.

It is highlighted that the original ornamentation pattern of mobile osteoderms in *Chlamyphorus truncatus* is very superficial and labile; in fact, it was difficult to recognize and describe it in the reviewed materials (Fig. 6.1). Two superficial depressions are clearly bordering a central higher

area, observable in the caudal portion of each osteoderm. In the context of this taphonomic evaluation, it is proposed that the contact with digestive acids accentuated the characteristics of the ornamentation from light to extreme (Fig. 6.2–15), including the increase in depth of the depressions and the decrease and rounding of the central area (Fig. 6.10).

Concerning different taphonomic attributes, irregular fractures are identified in each osteoderm; as result of fracture processes, different portions of osteoderms are present within the total sample. Osteoderm edges and fracture edges are mostly rounded, as a result of digestive corrosion (Fig. 6.11–12).

In the anterior portion of the digested mobile osteoderms (mainly those of the last mobile rows), a pointed area is observed, which gives them a pentagonal appearance (Fig. 6.2, 5, 8, 10). The area of imbrication of the osteoderms is thinner (Krmptotic *et al.*, 2024, fig. 4b, d) whereas the middle zone of each osteoderm is thicker, which is probably the reason why the digestive acids take longer to affect this area. In a more advanced stage of digestion, it is observed that the two superficial depressions that limit the central figure become finer until they disappear (Fig. 6.9–14). Another observed characteristic is

the desquamation of the surface (Fig. 6.14–17), interpreted as a product of digestive action.

Pichi, *Zaedyus pichiy*. This species is a small Euphractinae endemic to Argentina and Chile (Fig. 7.1) that can be distinguished from other armadillos by their marginal osteoderms, with sharply pointed apices and a light colored longitudinal dorsal line, extending from the posterior end of the scapular shield or the first mobile row to the posterior end of the pelvic shield (Fig. 7.2). As in other armadillos, all osteoderms are covered by cornified scales. Usually, seven mobile rows (range 6–9) separate the scapular and pelvic

shields, and one complete mobile row of nuchal osteoderms is present between the cephalic shield and the scapular shield (Fig. 7.2–6); this nuchal row has a triangular shape in dorsal view (Wetzel, 1985; Superina, 2008). Montalvo *et al.* (2016: tab. 4) totalized 782 osteoderms in a carapace of *Z. pichiy*, including 90 of the cephalic shield, 237 of the scapular shield, 270 of the mobile rows, and 185 of the pelvic shield (Fig. 7.3–6).

The osteoderms of the mobile rows present an articular portion without ornamentation and another portion with an ornamentation including a long and straight central figure,

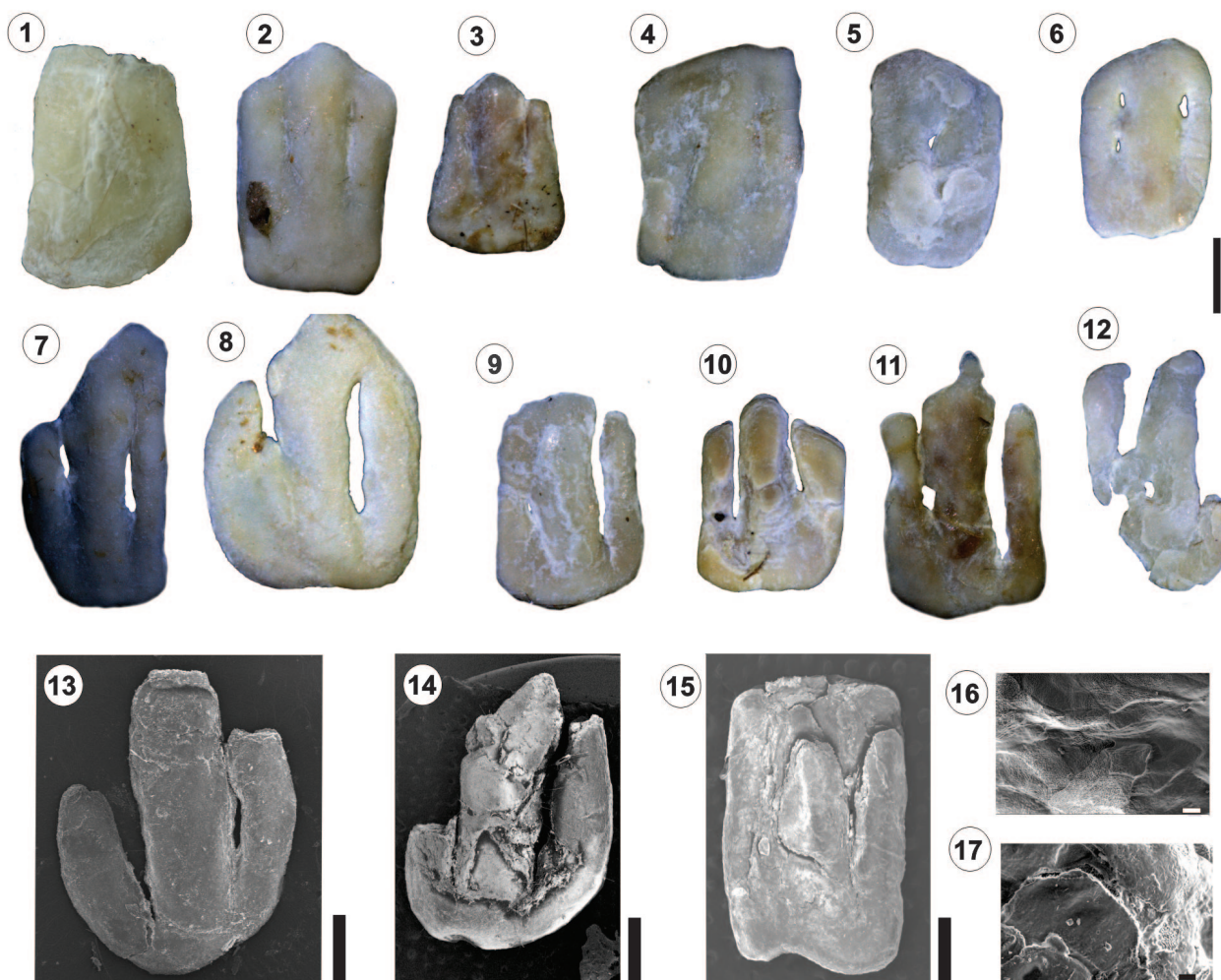


Figure 6. *Chlamyphorus truncatus* isolated osteoderms with digestion in external view; 1, Light modification; 2–6, Moderate modification; 7–10, Heavy modification; 11–12, Extreme modification; 13, Osteoderm with heavy modification, including breakage in the anterior portion; 14, Osteoderm with extreme modification, including breakage in the anterior portion and desquamation; 15, Osteoderm with moderate modification, including desquamation; 16, MEB image showing heavy modification of the external surface of osteoderm; scale bar= 5 µm; 17, MEB image showing heavy modification of the external surface of osteoderm; scale bar= 3 µm. Scale bar=1 mm for images 1–15.

laterally surrounded by several peripheral figures (Fig. 7.7). There are small dorsal foramina at the intersection of the sulci that delimitate both central and peripheral figures. The posterior margin of these osteoderms has a single row of piliferous foramina, with the most conspicuous one placed in the middle. The osteoderms of the cephalic shield form a pattern that is unique for each individual (Fig. 7.3); it varies in size and shape, and lacks any figure or foramen (Superina & Abba, 2014). In turn, the fixed osteoderms of the scapular and pelvic shields are sub-square to rectangular, with an ornamentation pattern that includes a central figure that reaches the posterior margin, laterally and anteriorly surrounded by peripheral figures (Fig. 7.4–5).

In Don Rodrigo locality, one pellet contained 24 isolated osteoderms of mobile rows, in which mainly the ornamented portion was preserved due to the breakage at the level of the transitional area with the articular portion. The total osteoderms recovered represent 3% of the average

of the total number of osteoderms of a complete carapace of *Zaedyus pichiy*. The majority of these osteoderms showed an intact surface, generally shining. Some of them had the dorsal foramina barely enlarged, located in the sulci, which may indicate a slightly modified ornamentation; in some cases, the foramina were enlarged to such a level that they facilitate the rupture of the osteoderm in the area of the sulci, presenting an intensely modified ornamentation. Thin edges were present in several osteoderms that showed a transverse fracture; and an extreme thinning of the caudal border was observed in the most modified osteoderms (Fig. 8.1–6). Eleven osteoderms were very incomplete, with slightly modified ornamentation, and some of them presented the internal surface with evidence of digestive corrosion (Fig. 8.6). Three pellets from Vicente locality contained portions of the caudal armor whose osteoderms showed light evidence of digestion (only with slight shine) (Fig. 8.7–8). These portions retained articulated vertebrae,

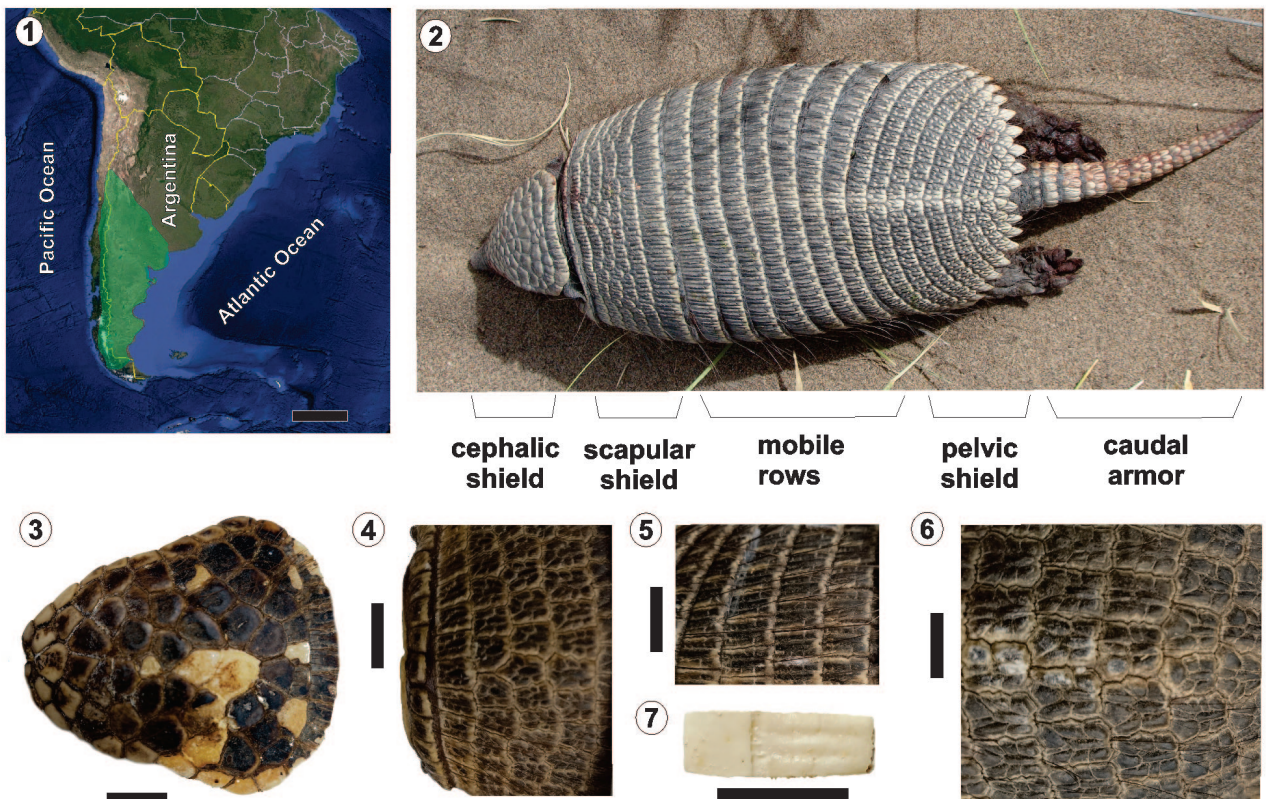


Figure 7. *Zaedyus pichiy*. 1, Distribution of *Z. pichiy* in Argentina and Chile; scale bar= 1000 km; 2, Dorsal view showing the different portions of the armor; 3, Cephalic shield in dorsal view; 4, Scapular shield in dorsal view; 5, Articulated osteoderms of the dorsal shield; 6, Pelvic shield in dorsal view; 7, Isolated osteoderm in external view. Scale bar= 10 mm for images 2–7. Image 1 from Landsat/Copernicus 2023; Google Earth, accessed December 2023.

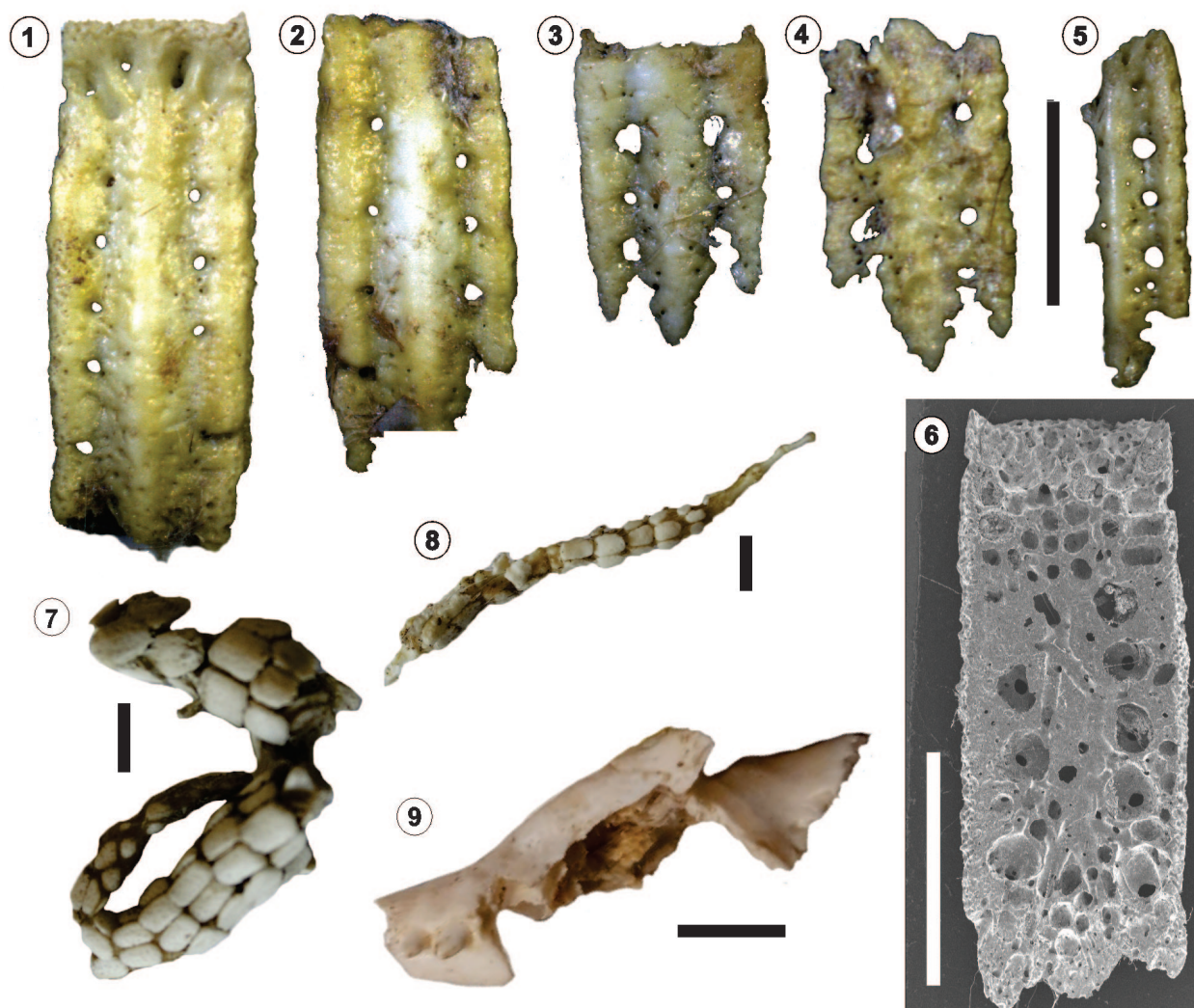


Figure 8. *Zaedyus pichiy*. 1–5, External view of isolated osteoderms from mobile rows with different degree of modifications (light to extreme) produced by digestion; 6, Internal view of isolated osteoderms from mobile rows with extreme modifications produced by digestion; 7–8, Caudal armors with articulated vertebrae and osteoderms in lateral view; 9, Cranial fragment with two molars without signs of digestion in ventral view. Scale bar = 5 mm.

one of which with light evidence of digestion. A pellet from Ventrencó locality contained a portion of armadillo cranial fragment with two molars without evidence of digestion (Fig. 8.9). Also, nine articulated vertebrae, two metapodials, and 12 undetermined bone remains were recovered from these pellets.

DISCUSSION

In Argentina, neotaphonomic studies of pellets, scats, and prey remains produced by different predators are frequent (e.g., Montalvo & Tallade, 2009; Montalvo *et al.*,

2011, 2016; Montalvo & Fernández, 2019; Guardia *et al.*, 2024), as they provide information to categorizing the producer, which can be used to interpret accumulations in the archeological and paleontological record. In some opportunities, this type of evaluation has also been helpful to recognize problems related to taxonomic misidentifications (e.g., Tomassini *et al.*, 2023), as well as to make biological and ecological interpretations of past organisms and faunal assemblages (Montalvo & Fernández, 2019).

Although leftover prey remains and occasionally pellets of *Buteogallus coronatus* have been extensively studied in

order to evaluate diet issues (e.g., Maceda *et al.*, 2003; Sarasola *et al.* 2010, 2022; Pereyra Lobos *et al.*, 2011), our evaluation constitutes the first taphonomic analysis of modifications produced on ingested prey remains. This new evaluation is compared with other previous taphonomic studies on this raptor bird, particularly focused on accumulations of leftover prey remains (Montalvo *et al.*, 2016; Guardia *et al.*, 2024). The sample evaluated herein includes remains of snakes, lizards, birds, and mammals (mainly armadillos) as both leftover prey remains and pellet content.

The studied pellets have provided abundant scales of snakes, hair remains, feathers, claws, and scarce bone remains, as well as plant remains, similar to the material commented by Guardia *et al.* (2024). These authors indicated that several prey remains recovered in the Ñancuñán area (Mendoza Province), with modifications attributed to weathering (mainly wind), correspond to old disaggregated pellets. The pellets recovered in La Pampa localities include Ophidia, one incomplete Avian bone, and remains of rodents and armadillos Euphractinae and Chlamyphorinae. These results are consistent with previous recognition of these taxa as an important part of *Buteogallus coronatus* diet (Pereyra Lobos *et al.*, 2011; Guardia *et al.*, 2024).

Only scarce rodent bones from Vicente nest locality could be analyzed following the traditional taphonomic methodology proposed by Andrews (1990). This nest provided 25 pellets (Tab. 1), four of which contained rodent remains of *Ctenomys* sp. and *Eligmodontia* sp., with low values of MNE, MNI, and relative abundance. The curve of relative abundance of rodents is similar to the averages obtained from samples originated by diurnal raptors and carnivore mammals (Fig. 2). Data from bone representation indexes, relative abundance, degree of breakage, and modifications by digestion on rodent bones recovered from *Buteogallus coronatus* pellets of Vicente locality indicate extreme degree of change related to digestion, and allows locating this predator in the category of extreme modification. However, Figure 2 reflects the representation of rodent skeletal elements recovered from one pellet from this locality that are assumed to belong to a single individual that was completely eaten, whose degree of digestion is light.

From digested osteoderms of *Chlamyphorus truncatus* and *Zaedyus pichiy*, different modification degrees are identified. Carapace fragments of *Z. pichiy* were the most frequent remains in nest localities from La Pampa and Mendoza provinces (Montalvo *et al.*, 2016, Guardia *et al.*, 2024). Characteristics of digested osteoderms of *Z. pichiy* recovered from pellets (scarce number from each pellet; disarticulation; shine in the external surface; modification of digestion more evident in internal surface, indicating that the cornified scale protected the external surface; Fig. 8.1–6) suggest that these elements could have been accidentally ingested.

From six pellets of Vicente locality and one pellet from Las Nutrias locality, digested osteoderms of *Chlamyphorus truncatus* showed different degrees of modifications and breakage, from scarce to high evidence, which resulted in changes of the original ornamentation (e.g., two superficial depressions bordering a central elevated higher area). A total of 319 dorsal carapace osteoderms were recovered from these pellets. This total number is low regarding the total number present in each carapace; it is possible that bone remains of each individual were incorporated in different pellets recovered on the same date from a same locality. In this sense, Raczynski and Ruprecht (1974) observed that the mixing of bones of one individual in two successive pellets is rare, but there are other mentions of consumed prey that were incorporated into different pellets (Laudet *et al.*, 2002; Woodman *et al.*, 2005). Laudet *et al.* (2002) suggested that multiple rejections of prey individuals could be more frequent than usually considered. If this behavior is verified in the case of *Buteogallus coronatus*, it would be a new raptor that generates multiple rejections of its prey.

It is highlighted that the original ornamentation pattern of thin osteoderms in *Chlamyphorus truncatus* is very superficial and labile. Barasoain *et al.* (2020) indicated that the ornamentation in *Chl. truncatus* is only observable in the cornified scale that covers the osteoderm. However, Krmpotic *et al.* (2024) and new observations in this study indicate that each mobile osteoderm has ornamentation in its caudal portion. Digestive action on these thin osteoderms has magnified their ornamentation. Several digested osteoderms showed desquamation of their surface, which can be

interpreted as a product of digestive action. It is interesting to note that, even in the most affected osteoderms, the woven bone described for these skeletal elements (Krmptotic *et al.*, 2024) is never exposed. With respect to the *Chl. truncatus* osteoderms recovered in the pellets studied here, we suggest that these armadillos could have been eaten whole or in parts, which would be linked to their small size and the presence of a thin, flexible, and highly vascularized carapace that facilitates the ingestion. This behavior is also suggested for ingestion of one rodent in Vicente locality (see above).

The typical pattern of integumentary system of armadillos is deeply modified in *Chlamyphorus truncatus* and, in particular, the scarce ornamentation of the thin osteoderms in the dorsal carapace may be related to its way of life (Krmptotic *et al.*, 2024). Barasoain *et al.* (2020) interpreted the presence of very thin osteoderms in the carapace as the result of a deossification process, developed over time as an adaptation to subterranean habits. This process would also have generated the partial loss of the ornamentation, since fossil chlamyphorines of Late Miocene show osteoderms with a marked ornamentation. The thinning and simplification of the osteoderms of *Chl. truncatus* complicate their preservation and identification. This may be a possible reason for their absence as prey of *Buteogallus coronatus*, except for occasional records (Parera, 2018, Barasoain *et al.*, 2020).

Chlamyphorus truncatus has been interpreted as a nocturnal species (Minoprio, 1945; Borghi *et al.*, 2011) and it is rarely observed in the field (Superina, 2011). Some information collected by one of the authors (MSK) from local residents (interpreted as an excellent source of information; Superina, 2006) confirms its presence during daylight hours in the same area of the nest localities studied here. *Buteogallus coronatus* is an early morning and crepuscular raptor, although biological information on this topic is scarce (see Sarasola *et al.*, 2022). The record of several pellets with remains of *Chl. truncatus* suggests that the range of activity of this armadillo outside its burrow would be longer than that indicated until now. The present study evidences that two vulnerable species (*B. coronatus* and *Chl. truncatus*) interact in their common distribution range (Central or Subandean Zoogeographic Domain *sensu* Ringuelet, 1961), increasing our knowledge about them.

Pellets from Vicente and Ventrencó localities contained cranial and postcranial elements of *Zaedyus pichiy*, and digested osteoderms of this armadillo were identified in pellets from Don Rodrigo locality. This armadillo is a common prey of *Buteogallus coronatus* (Maceda, 2007; Pereyra Lobos *et al.*, 2011; Montalvo *et al.*, 2016; Sarasola *et al.*, 2022; Guardia *et al.*, 2024). The recovered digested mobile osteoderms showed different degrees of modification, from light to extreme, features that support classifying of *B. coronatus* as an extreme predator.

Other published cases of armadillos as prey remains correspond to undetermined osteoderms recovered from a sample associated with the catarthid *Coragyps atratus* (Cathartiformes) in the northeast of Patagonia (Argentina) (Ballejo *et al.*, 2012), and osteoderms of *Dasypus* sp. with a heavy (entire surface affected) to extreme (a very thin layer of bone) degree of modification obtained from an accumulation produced by a Cathartidae, in cave deposits from the Early to Late Holocene in southeastern Brazil (Ballejo *et al.*, 2022, fig. 3a, b).

Although armadillo osteoderms are frequently found in paleontological and archeological sites of South America, few studies focused on evaluating the effect of digestive corrosion on their surfaces. This deficiency has led to problems in performing taxonomic assignments and interpreting the primary origin of fossil accumulations (Ballejo *et al.*, 2022; Tomassini *et al.*, 2023). In fact, neotaphonomic studies of endo- and exoskeletal remains consumed by New World vultures have allowed the recognition of this type of raptor action in the Holocene fossil record (including armadillo osteoderms) of the Gruta do Presépio site in southern Brazil (Ballejo *et al.*, 2022).

Tomassini *et al.* (2023) described the modifications produced by *Puma concolor* (Carnivora, Felidae) on *Dasypus novemcinctus* osteoderms. The presence of digested osteoderms from *Zaedyus pichiy* and *Chaetophractus villosus* were mentioned for scats from *Pu. concolor* described by Montalvo *et al.* (2007) and López *et al.* (2023). In the sample evaluated by López *et al.* (2023), osteoderms and several skeletal elements of *Z. pichiy* were the most abundant in the scats, and the authors highlighted the great tolerance to the digestive action and thus, the potential of being preserved in the fossil record. In turn, Montalvo *et al.* (2007) suggested

that the ingestion of osteoderms would be accidental. Osteoderms of *Z. pichiy* digested by *Pu. coronatus* show lesser modifications than those digested by *Buteogallus coronatus*. This shows that different predators located in the same category (*sensu* Andrews, 1990) produce different degrees of modifications in skeletal elements of the same prey.

The armadillos *Zaedyus pichiy* and *Chaetophractus villosus*, as well as *Ch. vellerosus*, were recovered as leftover prey remains produced by *Buteogallus coronatus*. As in previous studies (Montalvo et al., 2016; Guardia et al., 2024), only skulls, mandibles, teeth, and carapaces were recorded. In addition, other recovered material includes reptilian, avian, and other mammalian remains. Absence or scarcity of other postcranial material as leftover prey remains were previously informed by Montalvo et al. (2016) and Guardia et al. (2024). Although further analysis on *B. coronatus* is necessary, it is not ruled out that the low representation of bone remains may be related to its high degree of digestive corrosion.

CONCLUSIONS

The results of this investigation highlight the importance of neotaphonomic studies, in this case contributing to increasing the ecological knowledge of *Buteogallus coronatus* and its prey, embracing reptiles (ophidians and iguanians), birds, and mammals (caviomorph and cricetid rodents, mustelids, mephitids, lagomorphs, and armadillos), which can be accumulated with little (from leftover prey remains) or extreme (from pellets) modifications in open-air sites located in the central arid and semi-arid region of Argentina.

Digested osteoderms of the pichi *Zaedyus pichiy* and the pichiciego *Chlamyphorus truncatus* present changes of the original ornamentation and thickness reduction. *Z. pichiy* was previously registered in leftover prey remains, but the record of *Chl. truncatus* as part of the *Buteogallus coronatus* diet is a novelty. Osteoderms of both taxa are extremely modified. As previously suggested, this analysis supports that, despite their modifications, osteoderms of *Z. pichiy* would become easily fossilized. In contrast, the characteristics and the degree of digestion of the osteoderms of *Chl. truncatus* would make their preservation difficult. With respect to these osteoderms, present only in the pellets, we suggest that the prey could have been eaten whole or in

parts, and the degree of osteoderm modification endorses the categorization of *B. coronatus* as an extreme modifier, a classification previously based on rodent prey.

This study is especially relevant because it involves two little-known and sympatric species, *Buteogallus coronatus* and *Chlamyphorus truncatus* (endangered and data deficient respectively, according to the IUCN), in an area where this armadillo is endemic. As modern analogous, when the predator-prey interaction is known, and the way the predator modifies the prey bones can be identified, the resolution of the agents and processes involved in the formation of the fossil record are improved. This is particularly interesting because *B. coronatus* lives in an area rich in open-air paleontological and archaeological sites, which contain fossil records of armadillos, including fossil fairy armadillos.

As *Chlamyphorus truncatus* inhabits sandy plains and sand dunes in xeric environments of central Argentina, its conservation depends on the persistence of its arid and semiarid habitats. Everything that can contribute to the knowledge of the biology of both susceptible species (*Buteogallus coronatus* and *Chl. truncatus*) will help their conservation. Besides, it has been mentioned that *Chl. truncatus* is preyed upon by wild dogs and cats, but our study confirms that *B. coronatus* is another predator of this armadillo.

ACKNOWLEDGMENTS

We acknowledge the editors (F. Seoane, K. Borrazzo, and G. Hassan) and two anonymous reviewers, whose comments greatly improved the manuscript. To E. Cerdeño for her useful comments that improved the manuscript. We are grateful to M. Santillán and P. Tallade (Museo Provincial de Historia Natural, La Pampa, Argentina) for enabling collection access. This work has been funded by 21G projects from Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Argentina; from PICT-2018-00959 and PICT-2021-00034 from Ministerio de Ciencia y Tecnología of Argentina, and from Ministerio de Ciencia e Innovación of Spain (PID2021-126933NB-I00). This is a contribution included in the research line of TAPHIOS (TAPHonomic Investigations On Skeletons) group.

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doi: 10.5710/PEAPA.13.05.2025.529

Recibido: 9 de febrero de 2025

Aceptado: 13 de mayo de 2025

Publicado: 20 de octubre de 2025


RECURRENT DEATHS OF GUANACOS (*LAMA GUANICOE*) DUE TO WINTER STRESS IN SOUTHERN PATAGONIA: AVERAGED SAMPLES AND CHANGE OF ANALYSIS SCALES

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Abstract. Actualistic taphonomic observations of guanaco carcasses resulting from two winter mass death events that occurred in 2020 and 2023 at various locations in the Coyle–Gallegos River interfluvium (Santa Cruz, Argentina) provide valuable information about the formation of the fossil record. In this paper, we discuss how studying these die-offs allows us to monitor the formation of the so-called averaged samples. The longitudinal monitoring of carcass assemblages aggregated in different years forced us to change the scale of analysis, which gradually approached a controlled averaged sample. In this long-term study, we evaluate the main variables involved in the processes of guanaco carcass accumulation, such as the regularity and causes of massive accumulations, the locations of dead guanaco concentrations, the spatial superposition of deaths, and the variation in the size of bone patches due to processes such as carnivore action, trampling, and gravity sliding. For the analysis, we used the concepts of accumulation cycle, *tempo*, settling in, fossil stability, formational forcing, and retarding factors. Our results allow us to propose various conditions of bone preservation and identify spatial sectors with better burial opportunities, which are useful for constructing long-term viable analogous models, the usual ones of the archaeological and paleontological records.

Key words. Actualistic taphonomy. Bone accumulations. Massive deaths. Generic and specific redundancy. Settling in. Accumulation cycles. Patagonia.

Resumen. MUERTES RECURRENTE DE GUANACOS (*LAMA GUANICOE*) POR ESTRÉS INVERNAL EN EL SUR DE PATAGONIA: MUESTRAS PROMEDIADAS Y CAMBIO DE ESCALAS DE ANÁLISIS. Las observaciones tafonómicas actualistas de carcasas de guanacos resultantes de dos muertes invernales masivas ocurridas en los años 2020 y 2023 en una variedad de localizaciones en el interfluvio de los ríos Coyle–Gallegos (Santa Cruz, Argentina), ofrecen valiosa información acerca de la formación del registro fósil. En este trabajo discutimos cómo el estudio de estas muertes nos permite monitorear la formación de lo que se denominan muestras promediadas. El seguimiento longitudinal de conjuntos de carcasas que se agregaron en distintos años obligó a cambiar las escalas de los registros, los que fueron aproximándose a una muestra promediada controlada. En este estudio a largo plazo se evalúan las principales variables que intervienen en los procesos de acumulación de carcasas de guanacos, tales como la regularidad y las causas de las acumulaciones masivas, las localizaciones de las concentraciones de guanacos muertos, la superposición espacial de muertes y la variación en el tamaño de los parches óseos por procesos como la acción de carnívoros, el pisoteo y el deslizamiento por acción de la gravedad. Para el análisis empleamos los conceptos de ciclo de acumulación, *tempo*, *settling in*, estabilidad fósil, forzantes formacionales y factores retardatarios. Nuestros resultados permiten proponer diversas condiciones de preservación ósea e identificar sectores del espacio con mejores oportunidades de enterramiento, a fin de construir modelos análogos viables para escalas a largo plazo, las usuales del registro arqueológico y paleontológico.

Palabras clave. Tafonomía actualista. Acumulaciones óseas. Muertes masivas. Redundancia genérica y específica. *Settling in*. Ciclos de acumulación. Patagonia.

IN THIS PAPER, we will focus on methodological aspects of an actualistic study to discuss the criteria used in taphonomic and archaeological interpretations. Actualism refers to studying contemporary processes and their products to assign meaning to evidence from the past (Gifford-Gonzalez, 2018). Actualistic observations of guanaco (*Lama guanicoe* Müller, 1776) carcasses in the interfluvium of the middle basins of the Coyle and Gallegos Rivers (Santa Cruz province, Argentina; Figs. 1.1–2) are used to evaluate archaeological cases, highlighting the need to address the mixing of bones from naturally deceased animals with archaeological materials (Borrero, 1988; Massigoge *et al.*, 2015; Belardi *et al.*, 2022, 2025). There is limited concrete information about the conditions and rhythms involved in the formation of surface bone palimpsests and their eventual preservation in stratigraphy. Natural causes of massive bone accumulations typically include winter stress and rapid cooling events, such as those examined here, although examples of this type of death are rare in the literature compared to deaths resulting from floods, sediment flows, droughts, bogging, trapping, or other phenomena (Behrensmeyer & Hook, 1992; Rogers & Kidwell, 2007).

We present the current status of a study on recurrent winter stress deaths of guanacos, which allows us to monitor the formation of bone assemblages that can be considered averaged. This case is particularly suitable for discussing the conditions under which modern bones are incorporated into the fossil record and create mixtures with archaeological materials (Belardi *et al.*, 2025). Our survey began with observations in 2020 and systematic records from 2021 to the present. The deaths resulted from cold waves occurred during the winters of 2020 and 2023. Belardi *et al.* (2025) published detailed discussions of the 2020 mass accumulation in the different environments of the interfluvium. According to the Río Gallegos airport weather station, which is the closest to the study area, in 2020, there were three cold waves, and in 2023, only one, whose duration in days was longer (6 days) than the longest event in 2020 (4 days). Additionally, the maximum and minimum temperatures of the 2023 cold wave were more severe, with a maximum of 0°C and a minimum of -14.7°C (Bonfili, 2024). As we will see below, these conditions intensely affected the guanaco population in the region.

The interfluvium of the middle basins of the Coyle and Gallegos Rivers

The steppe landscape between the Coyle and Gallegos Rivers was shaped by glacial action (Ercolano *et al.*, 2016). Consequently, erosion is more prevalent than deposition on the terraced plains, leading to limited soil development. The region experiences a cold temperate climate with an annual temperature range of 0°C to 12°C. Winters are cold to very cold, influenced by polar and subpolar winds, resulting in substantial snow accumulation (Oliva *et al.*, 2001).

A characteristic of the region is the prevailing westerly winds, with an average speed of 4.6 m/s and a maximum speed of 360 m/s (Ercolano *et al.*, 2016). Annual precipitation values range between 200 and 300 mm. The landscape corresponds to the Terraced Levels Unit (Rial, 2001), comprised of alluvial levels of sedimentary material forming extensive blankets that have gentle relief between elevations 138 and 170 masl. In the plains of the terraced levels, some depressions act as shallow lakes, mainly dependent on the snow load. The soils are about 30 cm thick and have a 10 cm A1 horizon of sandy loam texture with abundant organic matter. The remaining 20 cm are clayey and correspond to the B2 horizon, which rests on rocks (Rial, 2001).

In the terraced levels, there is a maar of approximately 1 km², a product of regional volcanism and canyons carved by runoff that dissect them (Rial, 2001). The largest canyon is the Mack Aike. Its headwaters are at 160 masl, and its confluence with the Gallegos River is at 66 masl. It has an approximate extension of 29 km and a wide valley (between 150 and 390 m) through which a permanent watercourse flows. Its bottom is between four and 13 meters below the level of the plains, providing shelter and an important supply of pastures. The frequent use of the canyon by guanacos means that they die here more frequently than in other areas, regardless of extreme winter stress events.

The southern part of the study area corresponds to the northern limit of the Pali Aike Volcanic Field. Here, the basaltic lava flows, and volcanoes offer shelters such as walls, rock shelters, and caves that, together with the erratic blocks, were used by hunter-gatherer populations (Bird, 1988; Barberena, 2008; Borrero & Charlin, 2010).

The typical plant community in the area is the dry grassy

steppe, dominated by the Fuegian coiron (*Festuca gracillima*), accompanied by grasses or small herbs such as *Rytidosperma virescens* and *Carex andina*. Additionally, shrubs like *calafate* (*Berberis microphylla*) and *mata negra* (*Mulguraea tridens*) are present (Prieto *et al.*, 1999; Oliva *et al.*, 2001; Oyarzabal *et al.*, 2018). The main fauna includes guanacos, carnivores such as the puma (*Puma concolor*), the red fox (*Lycalopex culpaeus*), and the gray fox (*Lycalopex griseus*). Bird species

found in the area include the rhea (*Rhea pennata*), the caracara (*Caracara plancus*), and the black-chested buzzard-eagle (*Geranoaetus melanoleucus*) (Albrieu & Ferrari, 2000; Manero, 2000).

MATERIALS AND METHODS

The study presented here involved systematic field observations of two massive winter kills of guanacos that

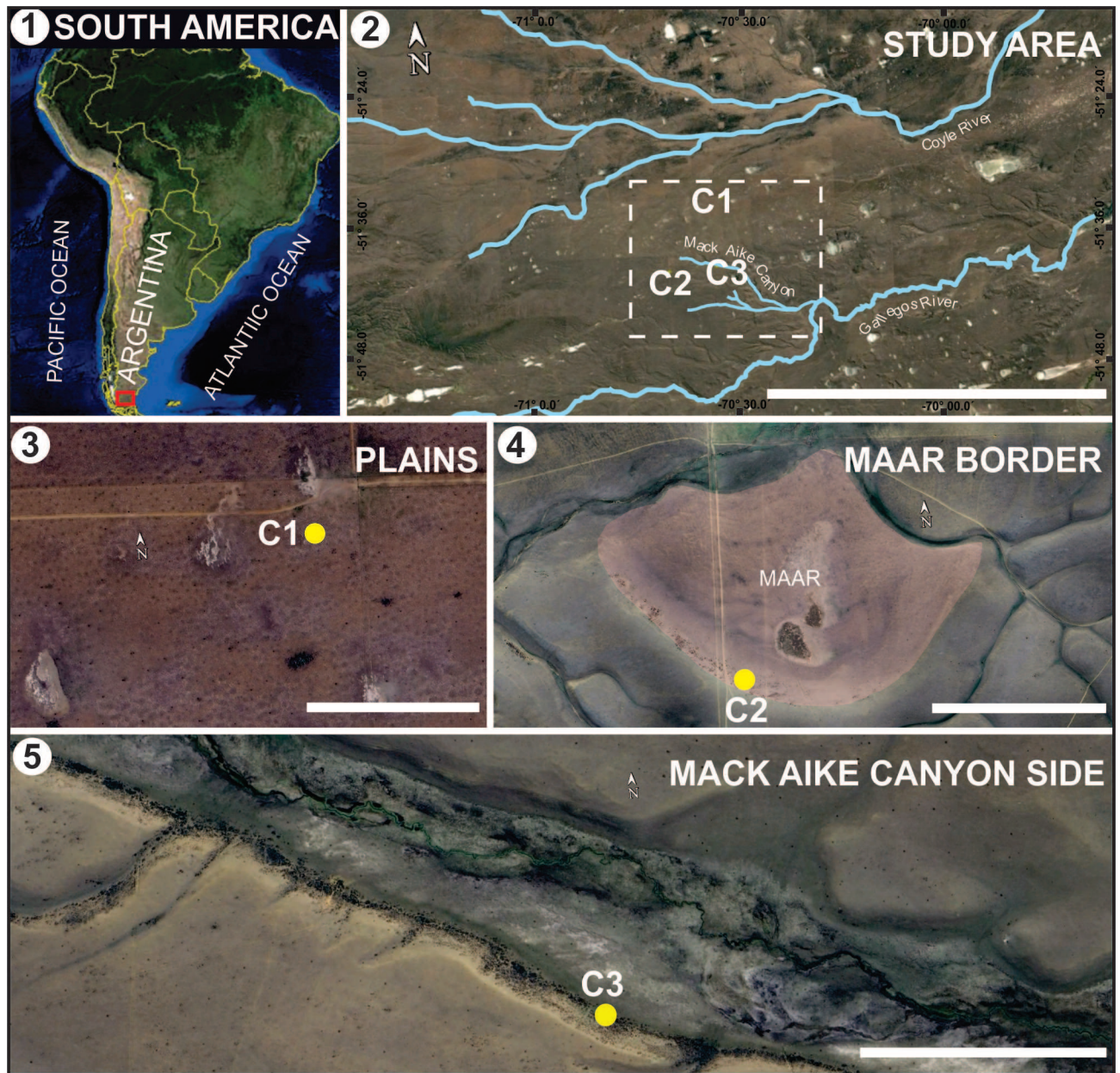


Figure 1. Study area where taphonomic observations are carried out; 1, Location of the study area in South America; 2, Detail of the study area and studied concentrations (Scale bar= 700m); 3, Detail of the location of Concentration 1 (Scale bar= 300m); 4, Detail of the location of Concentration 2; the orange shadow indicates the maar area (Scale bar= 700m); 5, Detail of the location of Concentration 3 (Scale bar= 450m).

occurred in 2020 and 2023 and were surveyed over five years (2021–2025) in the Coyle-Gallegos Rivers interfluvium. Samples were collected from three distinct sectors: plains, maar border, and Mack Aike Canyon side (Figs. 1.3–5). Our observations were made during the austral summer, between February and March of each year. Information was collected using variable size transects depending on accessibility, visibility, and distribution of carcasses. All isolated individuals and concentrations were georeferenced. Sex, age, weathering stage (*sensu* Behrensmeyer, 1978), degree of disarticulation, and carnivore action were determined for each individual. Mortality profiles were constructed for the samples from the different sectors. A soil penetrometer was used to judge the feasibility of burial in each sector. Samples for genomic analysis were also collected in 2021 and 2022 (Leggieri *et al.*, 2024).

In each sector, guanaco carcasses that appeared isolated or concentrated (two or more individuals) were counted and examined. Three concentrations, one in each sampled sector, were selected for longitudinal monitoring, or long-term follow-up of specific carcasses to register changes in different variables.

In this paper, we present and discuss in more detail the results of the monitoring of one of the plains concentrations (Concentration 1), where we were able to record different events of mass and individual deaths. Comparisons were made with concentrations from the other two sampled sectors: Concentration 2 (maar border) and Concentration 3 (Mack Aike canyon side), which vary significantly in their topography. This variation informed us, among other things, about the conditions for preserving skeletal remains, the potential fossil stability associated with burial, and the recognition of aggregation behaviors leading to mass deaths. We discuss the *tempo* of accumulations in Concentration 1, which refers to the duration of the process from the deposition of the carcasses to their complete recycling or burial of the bones. This information is evaluated in relation to potential cycles. For this purpose, among other concepts, the settling in effect is used, formulated on an experimental basis (Petraglia & Nash, 1987), with confirmations in several cases of systematic regional records (Bernáldez Sánchez, 2009). In the case of Concentration 1, settling in refers to the moment when, after the relatively

accelerated changes undergone by the carcasses during the initial months after snow melting, decomposition, disarticulation, and displacement by carnivore activity and other processes seem to slow down, and the bones begin to stabilize as time goes by.

This is due to the elements reaching a state of equilibrium or stasis with the environment and local meteorology. Although it does not imply the interruption of processes, it basically refers to a marked decrease in horizontal displacements and vertical migration. In a way, this is related to the concept of retarding or decelerating factors of environmental dynamics; for example, the effect of snow or shrubs covering the bones. In our discussion, we will add other factors resulting from the particular dynamics of the accumulations produced by mass mortalities.

In our case study, the main formational forcing factors—understood as those agents and processes that make up the configuration of a fossil assemblage—are related to winter stress and generally involve accumulations of snow, cold, hunger, or their combination within a framework of shelter-seeking by the guanacos. The aggregation of carcasses in different years in the same places made it necessary to change the scales of the records. Over the years, longitudinal tracking of individual carcasses forming part of the concentrations, especially Concentration 1, became more complex, leading us to a coarser-grained assessment. While this might seem to be a problem, observations on longer scales, even if less precise, are useful insofar as they seek to reconstruct accumulation cycles over the long term. We also included deaths prior to our first observation of dead animals in 2020 to evaluate these long-term processes. This sample consists of 15 mandibles and other disarticulated elements displaying advanced weathering, which we believe correspond to individuals that were part of older winter kills. This inference is based on the presence of several 6–9-month-old guanacos (Fig. 2).

The search for cycles includes those dictated by the rhythms of the massive deaths and those dependent on the geomorphological characteristics of the death sites. These cycles involve factors that affect the exposure time of the carcasses and, therefore, their duration on the surface.

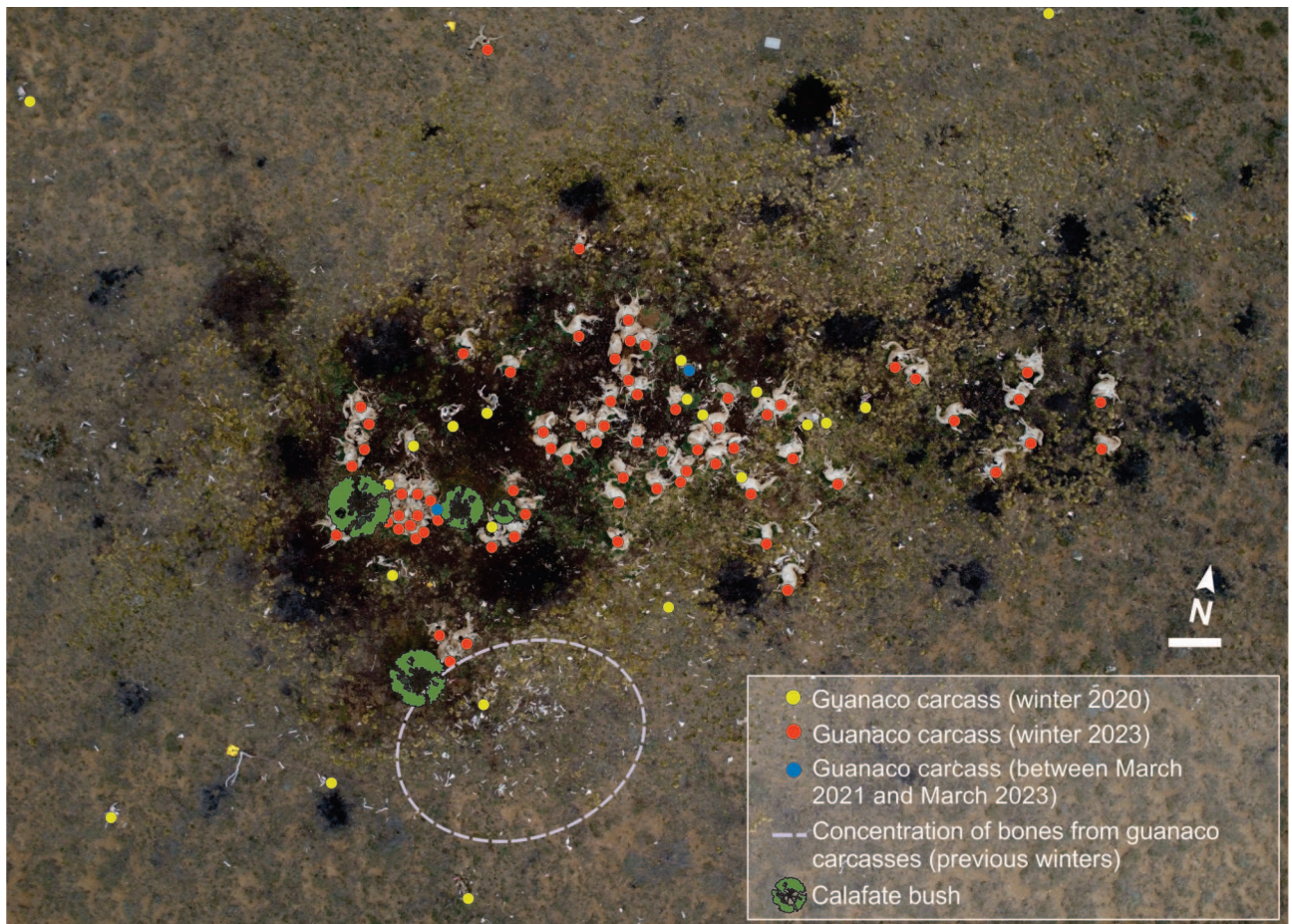


Figure 2. Distribution of dead guanacos around *calafates* during the winters of 2020, 2023, and pre-2020 in Concentration 1 (plains). Scale bar= 2m. Note the dung accumulation around and under the guanacos.

RESULTS

There were 945 guanaco carcasses assigned to winter stress deaths in the three sectors studied, distributed in the following events: winter 2020 ($n= 482$) and winter 2023 ($n= 463$) (Tab. 1). In general terms, the mortality profile of the total sample of winter 2020, analyzed in detail in Belardi *et al.* (2025), corresponds to selective deaths, with a significant number of first-year individuals. On the other hand, the profile of 2023 winter deaths resembles that of live populations with a significant number of prime individuals.

Plains

In this sector, large accumulations of carcasses are recorded, generally associated with the location of *calafate* bushes that are distributed in the form of patches. For example, in the death event of 2020, 19 concentrations

were recorded in this sector, five of which were composed of more than 20 individuals (Belardi *et al.*, 2025). On many occasions, the guanacos died in a lying position and huddled against each other (Fig. 3), a posture they adopt as a thermoregulatory mechanism that prevents heat loss by convection (de Lamo *et al.*, 1998; Lamuedra González, 2015). Over time, overlaps of carcasses associated with these locations were generated, configuring cases of generic redundancy, that is, depositions in the same space in general, without being specifically in the same *loci* (Hietala & Stevens, 1977).

In Concentration 1, 33 individuals corresponding to the deaths in the winter of 2020 were observed, most of them forming two groups, one around the *calafate* bushes and the other a few meters away from them (Fig. 4). We also observed the presence of a wide cover of dung of varying thickness (approximately 5 to 10 cm) as a result of the

TABLE 1 - Frequency of guanacos killed by winter stress in 2020 and 2023 recorded in different environments of the Coyle-Gallegos River interfluve.

Sector	2020	2023
Plains	255	334
Maar border	123	38
Mack Aike Canyon side	104	91
Total	482	463



Figure 3. Example of guanacos lying down, with their legs flexed and huddled against each other around *calafate* bushes in the plains sector.

defecation of, presumably, the individuals who took refuge in the area.

Longitudinal monitoring of these carcasses allowed us to record the disarticulation and displacement of anatomical portions due to the action of carnivores, birds of prey, and, possibly, trampling (Álvarez *et al.*, 2022; Belardi *et al.*, 2025). During our visits in 2022 and 2023, two new individuals were recorded and added to this concentration, and we cannot attribute them exclusively to winter stress. The

accumulation produced in 2023 in Concentration 1 as a consequence of a new event of winter stress was 69 carcasses, and again included individuals deposited around *calafate* bushes. This new death event created a mat of overlapping carcasses, with one from 2020 and others deposited in 2023 (Figs. 5.1–2). Other carcasses were also deposited at varying distances from the bushes (Fig. 2). This case of specific redundancy, or precise use of the same *locus* (Hietala & Stevens, 1977), is the main driver for the need to change



Figure 4. Drone image of Concentration 1 corresponding to winter 2020 deaths (photo taken in March 2022). Scale: the telescopic ruler seen in the image measures 2 m.

the scale of analysis in Concentration 1. Not only will the tracking of carcasses from the previous event —guanacos killed in 2020— be compromised after the last visit in 2025, but a stage begins in which, as a consequence of the progress of disarticulation and displacement of portions and bones, it will be increasingly difficult to recognize to which individual corresponds and consequently, to which death event each bone belongs. It is important to note that strict superimpositions, like those seen in Concentration 1, by adding fresh carcasses that begin their own accelerated period of disarticulation and decomposition, delay the processes underway on the previous carcasses deposited underneath, particularly the settling in effect. This delay is mainly the result of the overlapping carcasses limiting the access of carnivores to the carcasses deposited in 2020, which in turn, slows down the process of bone disarticulation.

Our observations and surveys in the plains report that the possibility of vertical migration of bones is minimal, given the poor penetrability (requiring between 9 and 26 strikes for a penetration of 5 cm) of the soils (aridisols), which is detrimental to their long-term preservation. The only form of potential burial is in the accumulations of dung near the bushes. The long-term preservation of such surface accumulations is short, so they only function in the short term. Although we have detected spatial overlaps of some archaeological materials with modern carcass concentrations along the transect in the plains, the potential for confusion of these short-lived palimpsests is very low.

Maar border

In this sector, the distribution of the carcasses is a little more homogeneous than in the plains, mainly due to the

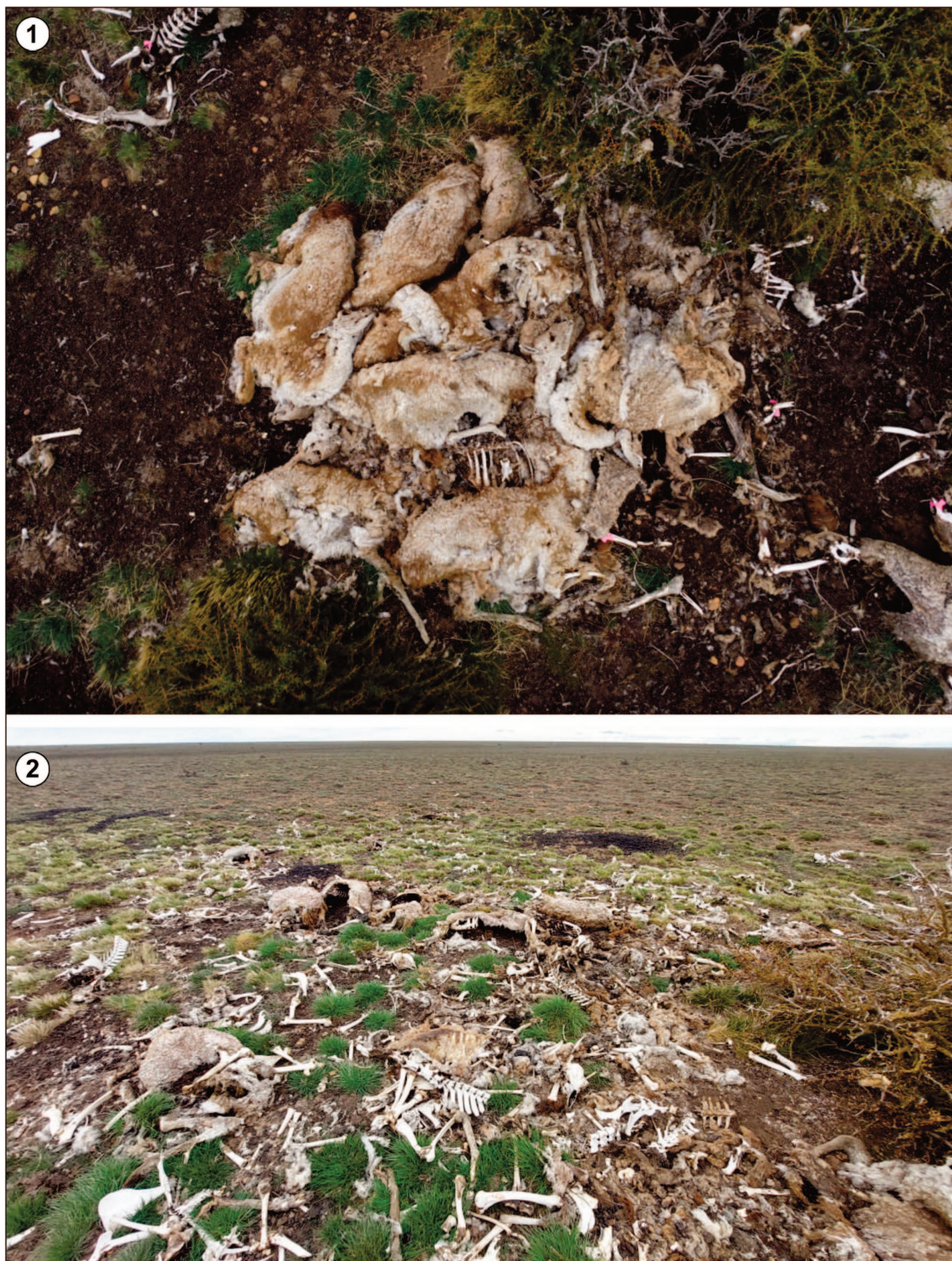


Figure 5. Examples of bone mats in the plains. **1**, 2020 and 2023 deaths in Concentration 1 (photo taken in March 2024); **2**, 2020 and 2023 deaths in another concentration with carcasses in the process of dispersal (photo taken in October 2024).

topography and the abundance of shrub vegetation (*calafate* and *mata negra*) that is more evenly distributed. In this location, we observed bone displacements not only due to the action of carnivores but also due to gravity acting in combination with surface water runoff. Longitudinal tracking of the 10 carcasses of the concentration monitored in this environment (Concentration 2), allowed us to detect displacements caused by the latter process (Fig. 6). The lack of sedimentation at the upper edge of the maar leads to low penetrability, requiring between 7 and 16 strikes for a penetration of 5 cm, while in the looser sediment of the talus 4 to 11 strikes are needed for the same mark. This situation, together with the slope of about 14°, creates favorable conditions for bone displacement. Some bones find their equilibrium point in topographic traps or bushes where the carcasses, articulated portions or individual bones are trapped, with good possibilities of burial due to the accumulation of fine sediment by wind and water action, or eventually reach the flat sector, where they may or may not be buried. Displacements occur, in many cases, along with gullies resulting from runoff. Recurrent passage of groups of guanacos and sheep (*Ovis aries*) trampling and kicking bones, aided by gravity, end up moving them towards the foot of the slope (Fig. 6). This process of reptation will produce a selective stabilization effect on the slope and at the foot of the slope. Over time, sedimentation and bioturbation (e.g., trampling) will lead to the burial of part of the skeletal elements in selected slope sectors, mainly at its foot. These varied conditions offer some alternatives for long-term preservation.

Mack Aike Canyon side

On the protected slope of the canyon, we observed less concentrated carcasses resulting from winter stress, also related to the presence of *calafate* and *mata negra* bushes. Longitudinal follow-up of the 10 guanaco carcasses from Concentration 3 showed that articulated portions and bones are displaced by the action of carnivores and gravity towards the canyon bottom, where better burial conditions exist due to wind and water sedimentation, pedogenesis, and trampling. Here, soil penetrability is high, with extensive areas where 4 to 6 strikes were needed for a penetration of 5 cm. The permanent presence of water on the canyon

bottom favors the growth of herbaceous vegetation (*mallines*), mainly composed of Cyperaceae, Juncaceae, and Poaceae (Peri *et al.*, 2024), leading to the development of soils with greater thickness (molisols) compared to other areas. These conditions favor long-term preservation, as evidenced by partially articulated and buried guanacos deposited since at least 4500 years BP (Belardi *et al.*, 2025).

In short, we found that burial possibilities are minimal in the plains (the primary focus of this study), moderate on the border of the maar, and higher in the Mack Aike Canyon side. Given the abundant and widely distributed archaeological record of the canyon, the high likelihood of burial may result in the formation of mixed assemblages of naturally deposited bones and artifacts (Belardi *et al.*, 2025).

DISCUSSION

The following evaluates the main variables involved in the accumulation processes of guanaco carcasses along the three concentrations.

Regularity of the phenomenon

Discussion of mass bone accumulations in the fossil record has highlighted that “*The long-term preservation and taphonomic signatures of a weather-related bone assemblage*”, including winter stress, depend on a variety of attributes that are difficult to predict (Rogers & Kidwell, 2007, p. 15), which is partly due to the limited research on these processes associating mass deaths with climate. A quick comparison with accumulations associated with water bodies or floods, which offer good burial and preservation conditions, suggests that instances of winter deaths with preservation potential are relatively rare (Rogers & Kidwell, 2007). However, in South America, we have good archaeological and paleontological examples of accumulations in aquatic environments, such as Paso Otero 1, Río Salado, or Ponsonby (Lepetz *et al.*, 2003; Gutiérrez & Kaufmann, 2007; Tonni *et al.*, 2008), but not of winter stress. Therefore, a fundamental question is whether these winter “climatic” deaths of animals constitute an unusual phenomenon. We think they are not. Not only have recent cases been recorded in Patagonia (Borrero, 1990, 2007; Estévez Escalera & Mameli, 2000; Rindel & Belardi, 2006; Vázquez, 2006; Belardi & Rindel, 2008), but also elsewhere in the world

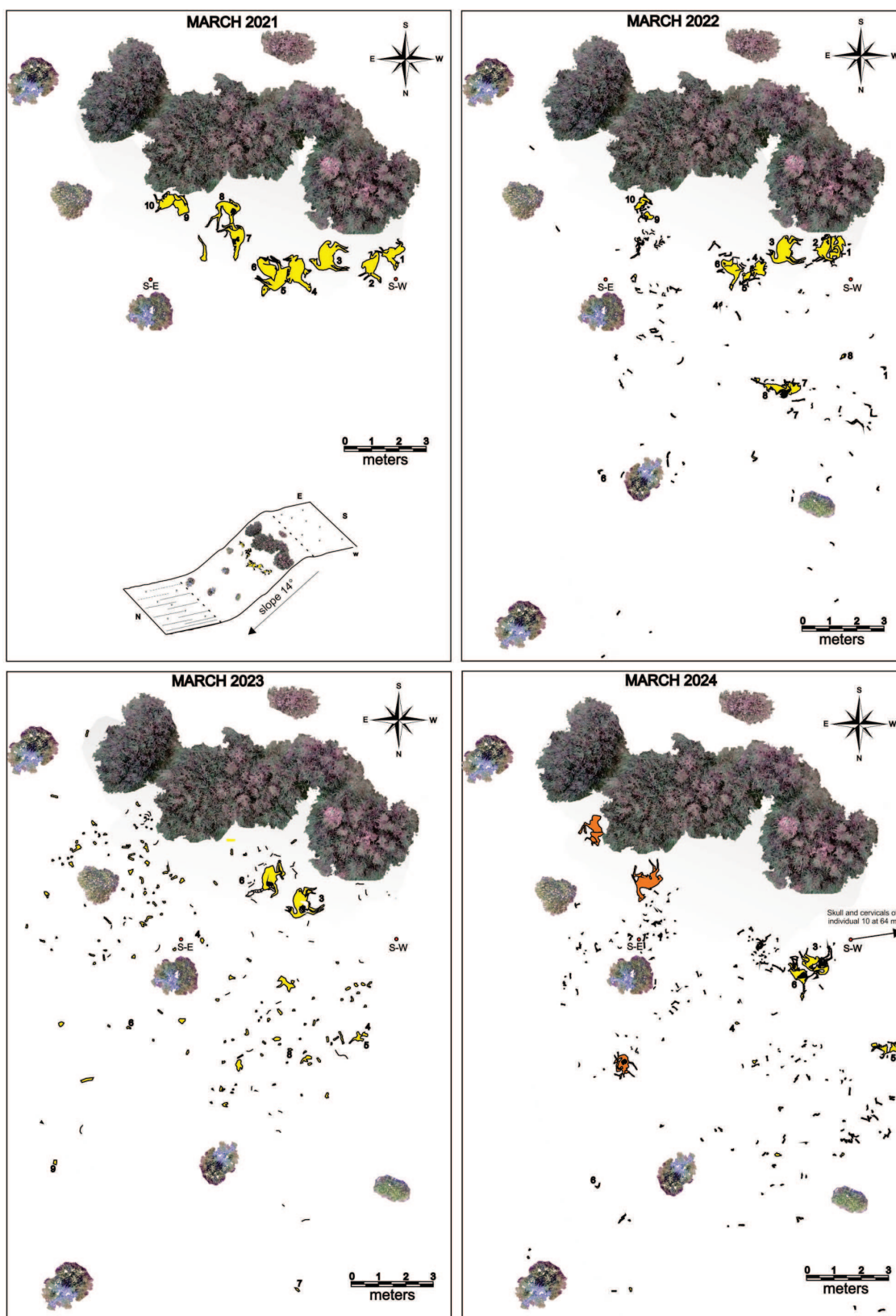


Figure 6. Diagram showing the process of disarticulation and dispersion slope down of the carcasses that form Concentration 2 (Maar border). The yellow carcasses correspond to the winter 2020 deaths and the orange ones to those of 2023.

(Martinka, 1967; Berger, 1983, 1986; Schallery Junrang, 1988; Weigelt, 1989; Okarma *et al.*, 1995; Scorolli *et al.*, 2006; Warchałowski *et al.*, 2015). In any case, the richness of bone accumulations in the Argentine Pampas has been highlighted (Weigelt, 1989), undoubtedly based on some important precedents, such as Darwin's observations on the coast of the Santa Cruz River. There, he observed concentrations of guanaco carcasses "*in certain circumscribed spaces, which were generally bushy*" ... "*beneath and amongst the bushes*" (Darwin, 1906, p. 159f.). These cases predate western cattle colonization, so they are not phenomena affected or caused by it. Darwin's observations show that the remains were abundant, showed no carnivore marks, and did not appear to have been transported. Later observations made in 1900–1901 near the mountain range (Prichard, 2003) confirm the phenomenon's importance and independence from livestock settlement. Similar observations were made even earlier by Bynoe on the shores of the Gallegos River (Darwin, 1906).

Causes

The causes of large winter climatic accumulations can be basically discussed in terms of the role of cold and hunger, both of which are associated with very cold winters, likely linked to previous summers with low productivity in pastures or significant droughts (Lamuedra González, 2015). These situations can be understood from animal physiology (Speth & Spielmann, 1983; Sturzenbaum & Borrelli, 2001; Belardi & Rindel, 2008). On the other hand, the parasitic load on animals in cold conditions, with low nutritional levels, is associated with massive mortality of guanacos in Cabo Dos Bahías, Chubut (Beldomenico *et al.*, 2003).

The starvation hypothesis proposes that when animals cannot migrate from the sectors most exposed to snow accumulation at the onset of snowfall, they starve. A paradigmatic case was presented by Johannes Weigelt (1989), who comments on the severe winters that affected wapiti (*Cervus canadensis*) in Jackson Hole (United States of America) at the beginning of the 20th century. Animals that could not migrate to the lowlands consumed hay, so they were hunted or moved to places without food. This case, although very old, is clearly affected by livestock expansion. But there are other cases not affected by human

activities, such as the mortality of bison (*Bison bison*) in Bighorn Basin (Wyoming, United States of America) in the winter of 1886–1887 (Frison, 2014) or others (Weigelt, 1989). In the Cabo Dos Bahías wildlife reserve, Chubut province, the mass death of 300 guanacos was recorded during the winter of 2000. The deaths were attributed to starvation following a severe drought that considerably limited the forage supply (Beldomenico *et al.*, 2003). In the particular case of our study, during fieldwork, we observed that several guanacos had vegetation in the abdominal cavity in the process of digestion, which leads us to think that starvation could not have been the cause of death. However, this is more complex to evaluate. On the other hand, the hypothesis linking deaths to sudden drops in temperature (Weigelt, 1989) is supported by certain characteristics observed in the assemblages. In our study, abundant guanacos seeking refuge in well-defined areas such as the bushes indicate that the animals arrived before this sudden temperature drop. Still, we have records from other locations in southern Patagonia that clearly reflect this phenomenon. The position of many of the animals in the surveyed assemblages (lying down with flexed legs; Fig. 3) and their stacking suggest events of synchronous deaths among many of them. However, both situations can occur in the same event. These alternative winter stress scenarios do not require empty stomachs (animals in poor nutritional condition). Though the overall nutritional status of the animals is an important condition that significantly impacts the threshold temperatures tolerated and the likelihood of survival in the low temperatures of extreme winters. The causes of death related to cold or starvation may be part of the same process that we could call multicausal (Weigelt, 1989).

Locations

Our observations show concentrations of carcasses on slopes that offer greater shelter and around *calafate* and *mata negra* bushes, a situation already observed in other Patagonian regions such as Cabo Dos Bahías (Lamuedra González, 2015) and related to the search for refuge during storms and wind protection. The proximity of molle (*Schinus molle*) bushes or rocky shelters functioning as attractors of carcasses has also been observed (Belardi & Rindel, 2008).

In any case, in our study, the association with bushes is dominant, as it constitutes the most ubiquitous refuge.

In Concentration 1, accumulations of guanaco dung were identified, forming a trail that ended in the *calafate* bushes. This trail implies the use of established access routes to these refuges, likely created by the simultaneous arrival of groups of guanacos or by the use of relatively snow-free areas due to successive arrivals. The surroundings of the bushes that concentrate the carcasses are characterized by a relatively continuous layer of dung of variable thickness.

Spatial overlapping

A characteristic of the samples from the interfluvium of the Coyle-Gallegos Rivers is the large number of overlaps of carcasses. The overlapping carcasses in different events and within the same event create large and relatively specific concentrations, including cases resembling a continuous mat of overlapping carcasses over previous concentrations. There are former modern records of animals stacked exactly one on top of the other at Lake Cardiel, at the Los Guanacos 3 rock shelter, where “*Only minimal portions of certain bodies were able to be seen because they were almost completely covered by other individuals*” (Belardi & Rindel, 2008, p. 47). The cases from the interfluvium plains record concentrations of a greater number of individuals and differ from previous records in Tierra del Fuego (Estévez Escalera and Mameli, 2000; Vázquez, 2006; Borrero, 2007). Regarding the number of deaths, the overlap of individuals and their effects, the case of 193 feral horses (*Equus caballus*) that died in a thunderstorm in the Tornquist Reserve, southwest of the Pampas region, is relevant. In the short span of two days between the event and the record, several groupings of carcasses were observed, some of which were partially trampled and buried in the mud (Scorolli *et al.*, 2006). This demonstrates that even on the scale of a single event, records of individuals can not only be difficult to control but can also create vertical displacements with the potential for long-term preservation.

Putrefaction and disarticulation

Although we will not delve into the details of the successive disarticulation of carcasses and some retarding effects of this process, we do not want to overlook some

observations. Mass die-offs, especially when they result in concentrated carcasses, slow down the disarticulation process (Burgett, 1990). Our case study, represented by carcass samples from the three sectors studied, is also comparable to that recorded by Todd (1987) for carcasses of cows (*Bos taurus*). This author describes that cows were stacked in a circular fashion seeking shelter in Plumbago Canyon (United States of America). Todd observed that the assemblage creates a “*unique taphonomic microenvironment*” (Todd, 1987, p. 109), in which carnivore action was concentrated at the edges (Todd, 1987) and uses it as an analog for studying bison from the Horner II site (Wyoming, United States of America).

Our case study also presents a particular pattern, similar to the one described by this author. Figure 7 shows schematically the distribution of carcasses from the 2020 kill event in Concentration 1. There is a semicircular distribution of scattered carcasses showing tooth marks away from the sector with the highest concentration of guanacos, most probably displaced by carnivores from the original deposition *locus*. The type and size of the marks, in addition to the presence of scats and footprints, allowed us to consider foxes as the main carnivore acting upon carcasses. The count indicates that 20 of 33 individuals in this concentration show carnivore marks (61%). Another striking fact is that 11 of the 20 guanacos are younger than 12 months (55%), especially those located in the semicircle in Figure 7.

Todd also notes that “*the proximity of carcasses*” (Todd, 1987, p. 147) conditions disarticulation patterns and that the rotting process “*often keep hide, particularly on the downward surface, moist and enhance its potential for rapid decay and consumption by invertebrate scavengers*”, leading to early disarticulation “*of the lower limbs through rapid deterioration of the surrounding hide ...*” (Todd, 1987, p. 149; see also Bernáldez Sánchez, 2009, p. 49). Observations at Wind Cave National Park, United States of America, on carcasses of buffalo (*Bubalus bubalis*) and other large and medium-sized mammals (Burgett, 1990) also showed that the lack of intense predator activity generates conditions for the persistence of microfaunal activity, particularly during the warm season when carcasses are not frozen. By comparing the preservation of the different bone concentrations generated by the mass death of guanacos

at the Paso Otero 1 site (Necochea district, Pampas region), Gutiérrez (2006) proposes that the spatial distribution of bones in discrete accumulations generated a differential microenvironment, with unique preservation characteristics for each of them. These microenvironments provided protection to the bones, accelerating or retarding the rate and intensity with which certain agents and processes acted on them (Gutiérrez, 2006).

In Concentration 1, carnivore activity constitutes an

accelerating agent of disarticulation and dispersal. In our second visit to this concentration, *i.e.*, 20 months after the 2020 mass death event, although half of the carcasses preserved their anatomical integrity and death position, we observed that some individuals suffered further disarticulation and dispersal of anatomical portions (*e.g.*, hind and forelimbs). Some skeletal portions were displaced up to 80 m from the original death site (Belardi *et al.*, 2025).

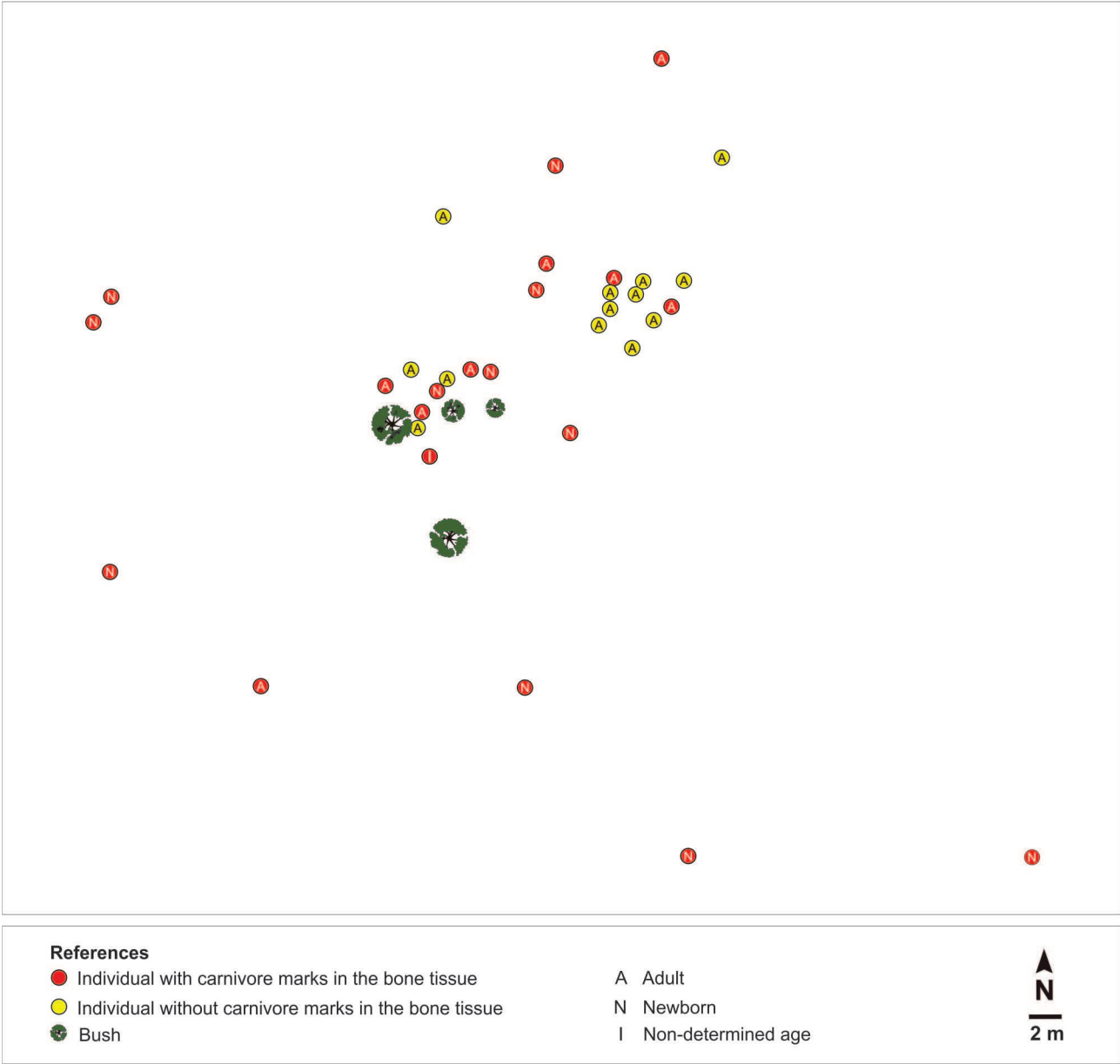


Figure 7. Schematic distribution of carcasses of dead guanacos in 2020 in Concentration 1. The red circles correspond to individuals with carnivore marks in the bone tissue.

Mummification

Part of the stabilization process in the guanaco assemblages seems to involve, in certain cases, natural mummification, probably favored by the dryness and wind that characterize the study area. Todd (1987) observed cases of natural mummification of dead cows in the boreal autumn that *"remained frozen in a bloat stage until the next April when night-time temperatures began to be consistently above freezing. By the time decay began in the spring, winds and sun had dried the // hide to a tough armor-like covering that has held the skeletons encased for at least 4 years"* (Todd, 1987, pp. 109–110). It is, then, a two-phase process that reaches an equilibrium upon mummification and eventually a second equilibrium after the reinitiated process of fragmentation and disarticulation. A similar situation was recorded with massively dead cows in Sierra Baguales in 2008, as well as in isolated guanacos in the Magallanes steppe, Chile (L. A. Borrero, personal observation), and has been systematically recorded and studied in the Puna (Nasti, 1994–1995).

Accumulation cycles

The duration of an accumulation cycle depends on a variety of formational forcing, erosion, trampling, rainfall (Todd, 1987; Wang & Martin, 1993; Bernáldez Sánchez, 2009) and retarding factors such as shade, vegetation cover, snow or ice cover, mummification potential, and traps limiting sunlight access (Behrensmeyer, 1978; Todd, 1987; Sutcliffe, 1990; Wang & Martin, 1993). Only long-term work can narrow down the influence of these different factors for any given area.

A cycle can be completed by the disappearance of the bones, either by total recycling or the action of other processes such as burial or transport by different agents. The alternative to burial eventually involves fossilization. Significant cycles can also occur without the disappearance of all the bones, as occurs in the cases of mummification just mentioned. The key to determining the length of such cycles is the settling in effect. The time to stasis is the *tempo* corresponding to a given combination of substrates, climates, and contexts, culminating in a relatively static state of things for a significant time. In the case of Concentration 1, the averaged sample was recorded and evaluated in

several stages, cumulatively, in which different forms of stasis are recognized. We learnt that these processes may took several months, particularly when harsh winters occur, thus retarding the stabilization phase. The final destination of practically all the samples recorded in the plains will probably be complete recycling, so these cases of stasis just constitute temporary phases. The study of winter deaths from Cabo San Pablo, Tierra del Fuego, ended when the bones of the carcasses deposited 17 years earlier could no longer be identified on the surface (Borrero, 2007), which does not imply that complete recycling has occurred, since there is evidence of vertical migration and burial of bones. In turn, at least part of the carcasses under study were covered by a beaver dam. When the area was revisited in 2005, 2010, and 2011, the beaver dams appeared progressively abandoned, and no bones attributable to the original carcasses could be detected, although many were initially marked with metal plates.

An alternative to consider is that the bones on the surface are constantly renewed with carcasses resulting from new deaths. A continuous bone rain, which refers to bones deposited as a result of natural deaths, seems unlikely, as any depositional hiatus exceeding 20 years will have virtually no bones on the surface, since that is the time required for the complete recycling of guanaco skeletons. The lack of evidence of mass death during the harsh winter of 2024 indicates that there are no linear processes and that directions can change so that the renewal of carcasses by new deaths need not be eternal. The long-term cycles of use of places by animals can change under a number of circumstances, and areas that now receive a continuous bone rain may just cease to receive it because the animals stop frequenting the area. In any case, the continuation of observations in the long term still has the potential to surprise us since we are exploring uncharted territory. At the same time, as we shall see, the information already recorded has good informative potential on a comparative scale.

Our observations on the maar border and the Mack Aike Canyon side should also be mentioned. The first case reports accumulation cycles on slopes. These present variations in bone preservation mechanisms, depending on the possibility of burial in the upper part. If this is limited,

there are numerous downslope depositional alternatives in topographic traps or bushes (see also Belardi & Rindel, 2008), so they are not merely continuous reptation avenues, a fallacy already recognized by Nash and Petraglia (1987). Their archaeological importance is well demonstrated (Martin & Borella, 1999; Ozán *et al.*, 2015).

On the slopes of the Mack Aike Canyon, we find the opposite case of the plains. The protection from severe climatic conditions (*e.g.*, strong and icy winds) offered by the sides of the canyon attracts both human occupations and guanacos. This sector is a place where there are both opportunities for burial and possibilities for burial to be relatively definitive. In other words, conditions are suitable for long-term preservation. Taphonomic evidence is complemented, in these cases, by fossil evidence, which not only records guanacos that have died of natural causes since the middle Holocene but also shows the preservation of articulated parts (Belardi *et al.*, 2025). Therefore, they allow us to evaluate to what extent the cases of sub-recent bones buried in articulated or disarticulated positions support previous studies on the “natural bone rain” that contaminates archaeological sites and also to recognize assemblages formed independently of human activity (Borrero, 1990; L’Heureux & Borrero, 2002). The cases of burials in the canyon are part of what we can see as contamination cycles, in which at least part of the stabilization process culminates in archaeological contexts.

CONCLUSIONS

The guiding question of this paper is what situations create spatial overlap of guanaco carcasses on the interannual scale, and what are the possibilities for bone preservation? Plains show the most repeated massive spatial overlap, but, at the same time, provide few burial opportunities, limited to short-term burial conditions that depend on dung accumulations. These conditions generally lead to total recycling. The stability cases observed, for example, due to spatial overlapping, are not definitive, as there are no conditions for open-air preservation. Temporary decoupling caused by specific overlays of carcasses and other retarding factors prolong these surface exposure cycles for a short time. We mention the alternative of deposition of new carcasses, in shorter time frames than

those granted by complete recycling. These potential cycles are summarized in a tension between weathering and the regularity of mass die-offs. But we also saw that even burial does not appear to be definitive in this area. These are assemblages that will inevitably continue to rearrange, transform, and recycle.

What are the characteristics of the averaged samples recorded? First of all, sedimentation in the plains is so low that it is difficult for them to enter the fossil record and contaminate eventual archaeological records. In any case, it would be very unlikely that eventual burial, if it occurs, would be cumulative or even definitive. Burial-exposure cycles are undoubtedly an essential part of the formation dynamics of the plains.

An important observation is that this negative evidence about the short duration of palimpsests-or even elements of them-in the plains is informative, particularly for archaeological finds at high altitudes related to obtaining lithic raw materials or other extractive tasks. In many of these cases, bones are not preserved due to low sedimentation, but activities related to the exploitation of faunal resources cannot be excluded. They should also serve to discuss models of human circulation in mountainous areas (Dawe & Kornfeld, 2017) or Martin’s (1973) invisibility argument.

Time and sedimentation rate are crucial in applying most mixing criteria. The latter variable seems to covary positively with the carcasses’ articulation and the elements’ bone integrity. We have proposed what appears to be a paradox. The large mass die-off event of the plains may remain hidden in the long term, while a contemporary one in the canyon with a lower frequency of die-offs may leave a detectable stratigraphic signal. What we know of other cases of mass die-offs also show the difficulties in detecting mass die-off in the Fuego-Patagonian area, since an event that seems much more visible, such as the San Pablo event where bone burial was demonstrated (Tierra del Fuego; Borrero, 1990, 2007), will hardly be recognizable as massive in the stratigraphic record given the scarce spatial overlap of cases.

The study of guanaco deaths due to winter stress from an actualistic perspective has allowed us to discuss the dynamics of fossil record formation processes and the

implications for the regional archaeology of Patagonia. Moreover, the unexpected taphonomic recurrence of death events in the same spaces opened new questions. It forced us to rethink our research, especially our contribution to the study of cycles and time averaging of bone accumulations.

ACKNOWLEDGMENTS

To the organizers of the 3° *Taller de Tafonomía Actualista de América del Sur*, held in Mar del Plata from October 7 to 9, 2024. We thank UNPA-UARG and INCUAPA-CONICET-UNCPBA for the institutional support to carry out our research; to the Bella Vista and Alquieta estancias (Santa Cruz) for their hospitality. To Natalia Alonso, Flavia Carballo Marina, Andrés Iparraguirre, and Leonardo Leggeri for their assistance in the field, and to Oscar Bonfili and Marcela Tonello for providing valuable information. Finally, we thank the reviewers for their careful reading of our manuscript and their many insightful comments and suggestions. The following projects have funded the research: UNPA 29/A476-1 (2021–2023), PICT 2018-0686, PICT 2021-01013, and UNCPBA 03-JOVIN-75F (2021–2022).

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doi: 10.5710/PEAPA.02.07.2025.543

Recibido: 13 de abril de 2025

Aceptado: 2 de julio de 2025

Publicado: 20 de octubre de 2025

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